Ontogeny, Intraspecific Variation, and Systematics of the Late Cambrian Trilobite *Dikelocephalus*

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ABSTRACT

Hughes, Nigel C.   Ontogeny, Intraspecific Variation, and Systematics of the Late Cambrian Trilobite *Dikelocephalus. Smithsonian Contributions to Paleobiology*, number 79, 89 pages, 47 figures, 11 plates, 27 tables, 1994.—Biometric analyses of well-localized specimens of the trilobite *Dikelocephalus* from the St. Lawrence Formation (Upper Cambrian), northern Mississippi Valley, suggest that all specimens belong to a single, highly variable morphospecies, *D. minnesotensis*. A complex pattern of ontogenetically-related and ontogeny-independent variation produced a mosaic of morphotypes, which show greater diversity than previously recorded within trilobite species. There is considerable variation within collections made from single beds. Variations of characters among collections are mosaic, and are clinal in some cases. Patterns of variation within *Dikelocephalus* cannot be related to lithofacies occurrence. There are no obvious temporal variations in *D. minnesotensis* within the St. Lawrence Formation, but some *Dikelocephalus* from the underlying Tunnel City Group may belong to a different taxon. The validity of this early taxon is questionable due to a lack of available material. The mosaic pattern of variation in *Dikelocephalus* mimics that documented at higher taxonomic levels in primitive libristomate trilobites, and helps explain difficulties in providing a workable taxonomy of primitive trilobites. Results caution proposition of evolutionary scenarios that do not take account of intraspecific variation. The recovery of dorsal shields of *Dikelocephalus* permits the first detailed reconstruction of the entire exoskeleton. The systematics of the genus is revised and twenty-five species are suppressed as junior synonyms of *D. minnesotensis*.

Contents

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Introduction

Dikelocephalus is a large asaphide trilobite that is abundant in Upper Sunwaptan (*Saukia* Zone) deposits of the northern Mississippi Valley (central to western Wisconsin, southeastern Minnesota, and northeastern Iowa) (Hughes, 1993). *Dikelocephalus* grew to a length of 40 cm or more and it has often been used as a textbook example of a Cambrian trilobite. In spite of this, the genus remains poorly described and no detailed reconstruction has ever been presented. The taxonomy of *Dikelocephalus* also remains poorly resolved and none of the wide variety of taxonomic schemes proposed (Owen, 1852; Walcott, 1914; Ulrich and Resser, 1930; Twenhofel, 1945; Rassch, 1951; Labandeira, 1983) has proved satisfactory. This paper is a comprehensive description of the morphology, intraspecific variation, and systematics of *D. minnesotensis* from the St. Lawrence Formation of Wisconsin, Minnesota, and Iowa. It is one of a series of papers that encompass the geological setting, taphonomy, population paleobiology, taxonomy, and functional morphology of the species (Hughes, 1990, 1991, 1993; Labandeira and Hughes, 1994). This paper provides documenation for the remarkable pattern of variation within *Dikelocephalus minnesotensis* Owen that has been briefly summarized elsewhere (Hughes, 1991). It also discusses the broader implications of these results for trilobite systematics and for questions about evolutionary mechanisms operating in the Cambrian.

GEOLOGICAL SETTING

During the Late Cambrian three broad lithofacies belts surrounded the exposed Laurentian shield (Palmer, 1960, 1965). Each of these lithofacies belts supported a distinctive

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range of trilobite biofacies (Taylor, 1977; Ludvigsen and Westrop, 1983a). Species of the family Dikelocephalidae inhabited shelf seas across much of North America during the latest Cambrian Sunwaptan Stage (Ludvigsen and Westrop, 1985), but the genus *Dikelocephalus* is mainly restricted to the inner-shelf mixed carbonate/siliciclastic belt. Its remains are found in large numbers only in the northern Mississippi Valley (in the sense of Dott et al., 1986) (central to western Wisconsin, southeastern Minnesota, and northeastern Iowa). This region is bounded to the south by the carbonate-dominated lithofacies, with distinct suites of trilobites, and to the north and west by the exposed Laurentian shield. This paleogeographic setting makes *Dikelocephalus* a suitable candidate for analysis of morphologic variation occuring within a single basin, as patterns of variation are unlikely to be affected by immigrations from other regions.

During the last three million years of the Cambrian Period *Dikelocephalus* was abundant and widely distributed throughout the northern Mississippi Valley (Figure 1). The oldest known *Dikelocephalus* were collected from the upper part of the Tunnel City Group (Figure 2). It occurs in both the very fine-grained, glauconite-rich feldspathic sandstones of the Reno Member (the uppermost unit of the Lone Rock Formation) and in its correlative nearshore facies, a fine-grained, non-glauconitic sandstone called the Mazomanie Formation (for discussion of lithostratigraphy see Ostrom, 1978). *Dikelocephalus* specimens are found most common within the St. Lawrence Formation, which directly overlies the Tunnel City Group (Figure 2). The principal facies in this formation is heterolithic, consisting of fine-grained clay-rich dolostones that are finely interbedded with feldspathic sandstones of very fine grain size. Specimens are occasionally found in laminated sandstone facies, which occur nearer to the paleoshoreline. The youngest known *Dikelocephalus* are fragments collected from medium-grained sandstones of the Van Oser Member of the Jordan Formation, which overlies the St. Lawrence Formation. *Dikelocephalus* occurs in the *Saukia*
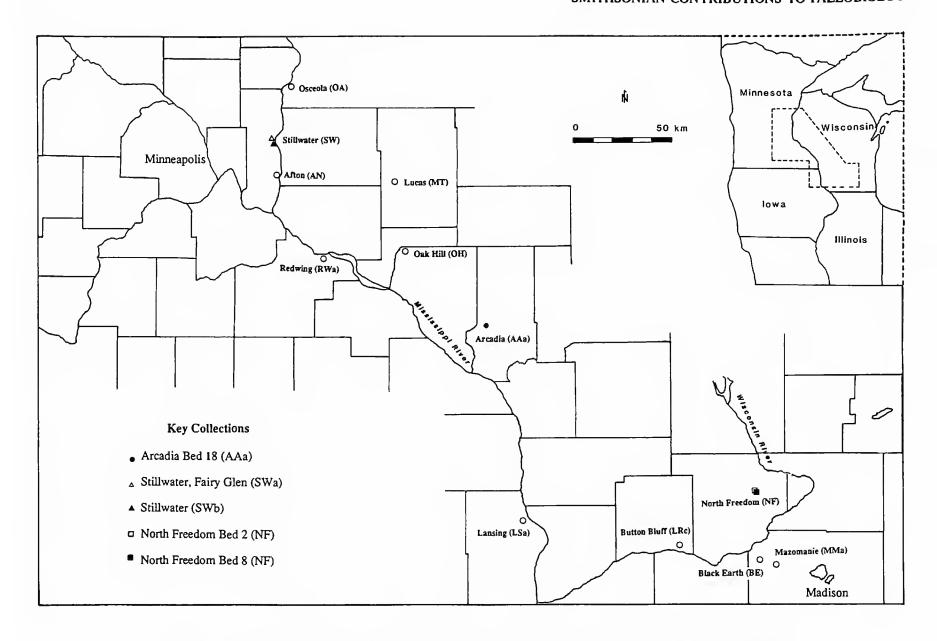
FIGURE 1.—Location of major collections of *Dikelocephalus minnesotensis* Owen from the St. Lawrence Formation. Key collections are those analyzed using multivariate statistical techniques. Approximate outcrop area of northern Mississippi Valley Cambrian deposits is shown in the top right corner. Full locality details are given in Hughes (1993).

Zone (in the sense of Raasch, 1951) of the Upper Sunwaptan Stage (Ludvigsen and Westrop, 1985), also known as the Trempealeauean Stage. Details of the stratigraphic and taphonomic distribution of *Dikelocephalus* in the northern Mississippi Valley, along with discussions of the mode of preservation and its effects on taxonomy, functional morphology, and paleoecology are provided by Hughes (1990, 1993) and Labandeira and Hughes (1994). These analyses have shown that the spatial and temporal distribution of *Dikelocephalus* from the northern Mississippi Valley is well understood and that the present distribution of specimens reflects the primary biological distribution of *Dikelocephalus*. Results suggest that *Dikelocephalus* from this region are suitable candidates for a detailed locality-based study.

PREVIOUS WORK

The genus *Dikelocephalus* when first described by Owen (1852) included a broad range of libristomate trilobites (in the sense of Fortey, 1990). None of Owen's species, other than *D.*

minnesotensis, are now assigned to the same family as *Dikelocephalus*. A series of works, based mainly on material collected subsequent to Owen's work, (Hall, 1863; Winchell, 1874) established the basis of the family Dikelocephalidae (Miller, 1889). Following Walcott's (1914) revision of the genus, Ulrich and Resser (1930) produced an extensive monograph in which twenty-six species of *Dikelocephalus* were described from the northern Mississippi Valley. This monograph has been criticized mainly on the grounds that the taxonomy of the group was subdivided too finely (Twenhofel, 1945; Raasch, 1951; Taylor and Halley 1974; Westrop, 1986). Despite the criticism there have been few attempts to reassess the status of *Dikelocephalus* species and additional species have been described (Bell, Feniak, and Kurtz, 1952). Raasch (1951) attempted a revision of dikelocephalid and saukiid trilobites, but this work consisted of a list of synonymies with little discussion and without illustrations. Raasch's (1951) revision also relied heavily on stratigraphic rather than morphological criteria. *Dikelocephalus* has since been recorded in other areas of north America (Grant, 1965; Winston and
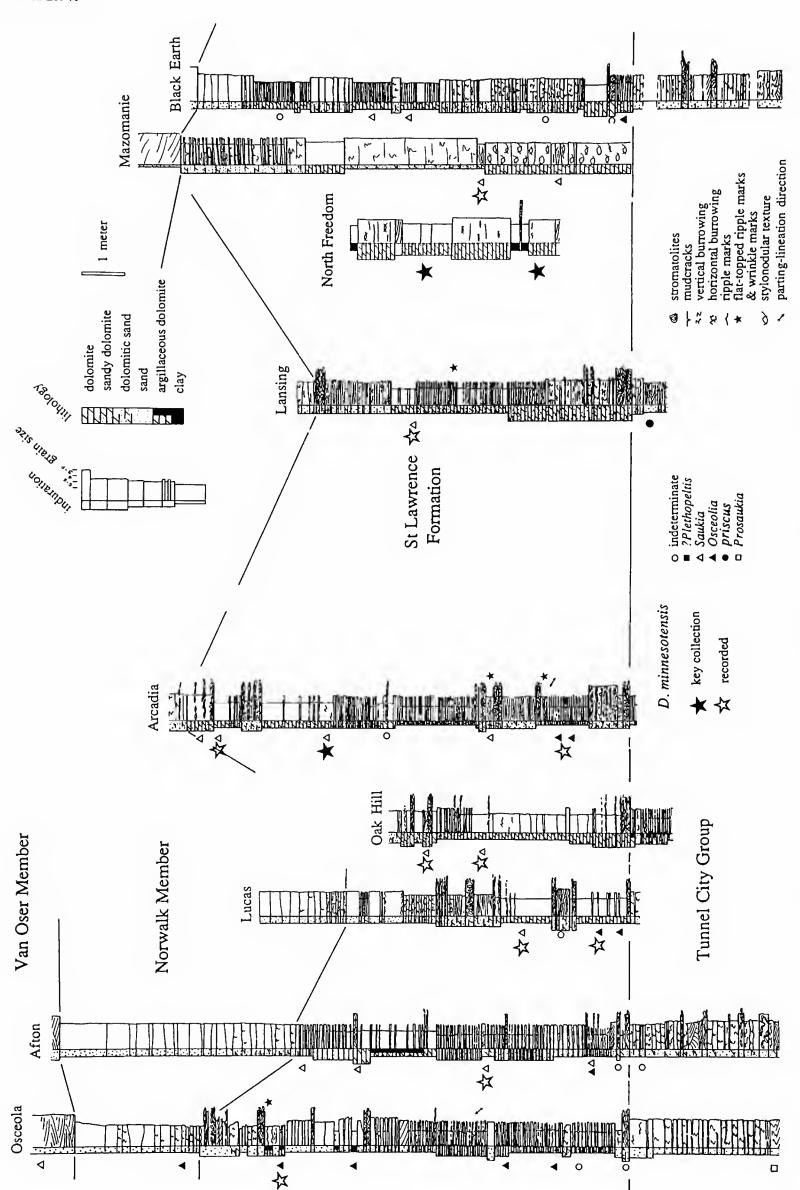
FIGURE 2.—Stratigraphic sections of nine localities from the northern Mississippi Valley. The sections lie along an approximate northwest–southeast transect. Occurrence of *Dikelocephalus minnesotensis* Owen is indicated by large stars. Closed stars indicate collections that have been analyzed using multivariate statistics. Open stars record the occurrence of *D. minnesotensis* at this horizon. Full locality details are given in Hughes (1993).

Nichols, 1967; Stitt, 1971; Westrop, 1986) but specimens have been usually identified only to the generic level.

Ulrich and Resser's (1930) approach to the systematics of dikelocephalid trilobites focused on character variability; almost any feature that showed morphological variation was automatically considered to be of taxonomic importance. The result was a large number of species descriptions based on minor and inconsistent differences between specimens. Later workers (e.g., Twenhofel, 1945) found this taxonomy impossible to apply to new material. Using the same suite of specimens that Ulrich and Resser (1930) described, Labandeira (1983) and Labandeira and Hughes (1994) quantitatively assessed the validity of these species designations. The results suggest that all specimens form part of a single morphospecies.

Ulrich and Resser (1930) also used some meristic characters in their species diagnoses. The distribution of some of these characters could potentially serve to define species within *Dikelocephalus*. The significance of these characters has not been previously re-assessed.

Finally, Ulrich and Resser's (1930) type suite was made up of material collected from a large number of localities. Many of these localities were represented by one or two specimens, and some of these specimens possess characters which could be species diagnostic. It is not possible to assess the taxonomic significance of these characters without understanding the range of variation within collections from single bedding planes. Hence it is impossible to resolve the taxonomic status of *Dikelocephalus* on the basis of Ulrich and Resser's type-suite alone (Labandeira and Hughes, 1994). The present study concentrates on new and well-localized collections to determine variation within *Dikelocephalus* and aims to resolve those characters that can be used to recognize discrete taxa.

A list of characters considered important for species recognition by previous authors (Table 1) documents a wide range of morphological variation within *Dikelocephalus*. Most of Ulrich and Resser's (1930) species descriptions were written as comparisons, rather than as diagnoses. These comparsions were not comprehensive, with the result that Ulrich and Resser's species descriptions are difficult to evaluate. Hence many of the characters listed in Table 1 were selected by observation of the type specimens of Ulrich and Resser's (1930) species, rather than from their original descriptions.

Approach and Methodology

APPROACH

The contrasting taxonomic schemes of Ulrich and Resser (1930), Raasch (1951), and Labandeira (1983) are indicative of the remarkable nature of variation in *Dikelocephalus*. Early taxonomic splitting highlighted the marked degree of variation in some characters (Ulrich and Resser 1930; Raasch, 1951), whereas bivariate analyses illustrated that many other characters are relatively invariant (Labandeira, 1983). In order to fully document the morphology of *Dikelocephalus* a more compre-

TABLE 1.—Morphological characters of previously described species and varieties herein assigned to *Dikelocephalus*. The characters were selected from published descriptions and from inspection of figured type material. See text for discussion.

Hall (1863)
variety *limbatus*
    border present
    caeca present

Ulrich and Resser (1930)
minnesotensis
    border slightly inflated
    frontal area wide
    medial portion of glabellar anterior straight
    angle of lateral glabellar furrows to sagittal axis acute
    subequally divided pygidial pleurae

barretti
    glabella and pygidial axis pustulated
    pygidium rounded

beani
    pygidial pleurae unequally divided

brevis
    palpebral lobes large
    frontal area very short
    posterolateral spines long
    pygidial pleurae equally divided

declivis
    median suture absent
    genal spines short
    free cheeks flat

edwardsi
    caeca present
    border present
    median suture absent

gracilis
    frontal area short
    maculae present
    median suture absent
    posterolateral spines long
    pygidial pleurae equally divided

granosus
    cephalon granulated
    palpebral lobes of high relief
    glabellar furrows firmly impressed

halli
    frontal area wide
    pygidial pleurae subequally divided

hotchkissi
    medial portion of glabellar anterior straight
    glabellar sides convergent
    palpebral lobe small
    angle of lateral glabellar furrows to sagittal axis obtuse
    free cheeks flat
    pygidial pleurae subequally divided

inaequalis
    pygidial pleurae unequally divided

intermedicus
    frontal area long, flat
    frontal area anterior margin rounded
    fifth pygidial axial ring present
    pygidial pleurae subequally divided

juvinalis
  small size
  frontal area short, wide

marginatus
  cranidial border present
  median suture absent
  pygidial furrows converge at base of posterolateral spine

norwalkensis
  cranidial border present
  frontal area anterior margin rounded
  glabellar furrows firmly impressed
  post-axial ridge present

orbiculatus
  cranidial margin rounded
  palpebral lobes large
  pygidium rounded

ovatus
  glabella wide
  pygidium rounded

oweni
  anterior margin of frontal area angular
  frontal area short
  palpebral lobes large
  pygidial pleurae unequally divided

postrectus
  pygidial posterior margin straight

raaschi
  frontal area narrow, flat
  palpebral lobes large
  median suture present
  pygidial pleurae unequally divided

retrorsus
  frontal area short
  occular platform narrow
  posterolateral spine long

subplanus
  frontal area anterior margin rounded
  median suture absent
  pygidium elongate

thwaitesi
  cranidial border present
  free cheeks wide

weidmani
  border present
  maculae absent
  pygidial pleurae unequally divided

wiltonensis
  border present
  glabella anterior margin rounded
  frontal area anterior rounded

wisconsinensis
  frontal area anterior rounded
  palpebral lobes large
  genal spine long
  pygidium rounded

Raasch (1951)
minnesotensis
  frontal area long, wide
  palpebral lobes small
  pygidial pleurae subequally divided

barretti
  cranidial border present
  faint caeca
  frontal area short
  median suture absent
  equally divided pleurae
  posterolateral spines long

inaequalis
  pygidial pleurae unequally divided

marginatus
  cranidial border present
  pygidial furrows converge at base of posterolateral spine

oweni
  no shared characters, separating this taxon from others, are apparent among Ulrich and Resser's (1930) type specimens that Raasch assigned to *D. oweni*

postrectus
  pygidial posterior margin straight

thwaitesi
  cranidial border present
  frontal area long
  unequally dividied pleurae

hensive approach is necessary. One possiblity would be a multivariate investigation of the entire suite of *Dikelocephalus* specimens. This approach was rejected because of (1) the fragmented condition of the majority of material collected previously, (2) the difficulty of interpreting the results of multivariate analyses based on "mixed-mode" data sets (those including both metric and non-metric characters), and (3) many collections with sample sizes too small to assess the degree of intraspecific variation.

To overcome these problems the analysis of variation in *Dikelocephalus* reported here proceeded in three stages. First, variations in nominal (presence/absence) and ordinal (ranked scale) characters were analyzed using specimens from throughout the northern Mississippi Valley. These characters were analyzed individually to permit recognition of their distinct patterns of variation within and among collections. Analyses did not reveal any consistent variations within the whole sample. Several seemingly discrete characters exhibit continuous variation. Some characters show size-dependent variation, and there is great morphological variability within collections from individual beds.

Having failed to detect consistent discontinuous variation within *Dikelocephalus* the resolution of the morphological analysis was increased. Quantitative analyses of collections from individual beds were used to examine details of holaspid growth and assess population-related variation. Bivariate analyses show significant allometry in holaspid growth. Patterns of intra- and intercollection variability are continuous and highly complex. The independence of many characters, combined with subtle population-related differences in growth rates, evidently results in a mosaic of morphologies, indicating high levels of plasticity within *Dikelocephalus*.

The third stage of the work was to examine whether there are

subtle patterns of covariance within the data set that were undetected in bivariate analyses. Multivariate analyses did not indicate morphological discontinuity within *Dikelocephalus*. Rather, it confirms the results of the other approaches, suggesting that many characters within *Dikelocephalus* vary independently.

SPECIES CONCEPT

The species concept employed in this study is "the smallest aggregation of populations ... diagnosable by a unique combination of character states in comparable individuals" (Nixon and Wheeler, 1990:218). Such phylogenetic species cannot be further subdivided even if they show considerable continuous variation within the lineages (Wiley, 1978).

METHODS

1. *Analysis of nominal and ordinal characters.* Some morphological variation within *Dikelocephalus* reflects variations in discrete characters, either presence/absence characters or characters that occur in a small number of discrete states. These are referred to as nominal characters. Other characters vary across a continuous spectrum but their exact position within this spectrum cannot be assessed quantitatively. Instead, only their relative or ranked position can be determined. These are called ordinal characters. Nominal and ordinal characters were analyzed in more than 2750 specimens from 93 localities in the northern Mississippi Valley (detailed in Hughes, 1993). In addition to features previously unrecognized in *Dikelocephalus*, analysis of nominal and ordinal characters included all the non-metric characters used by Ulrich and Resser (1930), who used these sorts of features extensively in their taxonomic study. Such characters formed the basis for some of their specific designations but were largely ignored by Labandeira (1983) and Labandeira and Hughes (1994) in their analyses of the type-suite.

2. *Bivariate analysis of collections from individual beds.* Bivariate analyses are particularly useful for investigating the growth dynamics of sclerite dimensions. Labandeira's (1983) bivariate study of Ulrich and Resser's material provided a valuable overview of bivariate relationships but did not examine growth controls or locality-related variation. Because the present study focuses on the growth- and locality-related controls of variation within *Dikelocephalus*, it is essential to perform detailed locality-based bivariate analyses.

3. *Multivariate analysis of collections from individual beds.* Multivariate analyses have been used to examine the relationships among sclerite dimensions, and to assess the overall similiarity among specimens. Multivariate anaylses are comprehensive methods of assessing morphological variation because a large number of characters may be analyzed synoptically, although results may be difficult to interpret (Palmer, 1985). In this study multivariate analyses were performed on samples from single beds which contained large numbers of specimens. Multivariate analyses were limited to samples of sufficient size to permit assessment of the range of intra-sample variation. Metric and angular data were included in the multivariate analyses, nominal and ordinal characters were excluded.

MATERIALS

Morphological variation in *Dikelocephalus* was assessed from about 1000 specimens collected during this study, combined with specimens held in 10 North American museums and universities (see Hughes, 1993), specimens belonging to Mr. Gerald Gunderson, and the Sauk County Historical Museum. In total, more than 2750 specimens were examined.

Collections with excellent locality data were used to analyze variation within and between collection of *Dikelocephalus*. Studies were concentrated on collections from single beds from six localities, all within the range of the *Saukia* fauna (see Hughes, 1990). The collections used were: North Freedom Bed 2 (NF2; quarry on west side of Mirror Lake Road, 0.5 km north of intersection with Hwy 136, 4 km north of North Freedom, Sauk County, Wisconsin), North Freedom Bed 8 (NF8; locality as NF2), Arcadia Bed 18 (A Aa; quarry on east side of Hwy 93, 4 km south of Arcadia, Trempealeau County, Wisconsin), Button Bluff Bed 6 of G.O. Raasch (1939) (LRc; quarry above Button Bluff Cemetary, 4 km east of Gotham, Richland County, Wisconsin), J.C. Ferguson's collection from Stillwater (SWb; roadcut on Hwy 95, 0.5 km north of Stillwater, Washington County, Minnesota), and LaGrange Mountain (RWa; east side of Hwy 61, town of Redwing, Goodhue County, Minnesota) (Figure 1). Full locality details are given in Hughes (1993). With the exception of Stillwater, each of these localities has been the subject of detailed sedimentological analyses by Hesselbo (1987) or Hughes (1990). Each collection contained a large number of well-preserved specimens, which were prepared in the laboratory using standard preparatory techniques. The localities were selected to give a broad geographic coverage of the region (as an example, Stillwater and North Freedom are approximately 300 km apart) (Hughes, 1993, fig. 2), and to illustrate possible temporal variation within the *Saukia* fauna times. The selection aimed to represent the onshore/offshore proximality trend and to parallel paleoshore line. Collections from different horizons at the same site were treated as separate statistical populations (i.e., North Freedom Beds 2 and 8; Stillwater a and b). In order to increase temporal resolution, a pooled sample of specimens from the Tunnel City Group was also include in the morphometric analyses (see Hughes, 1993, fig. 1). Small sample sizes prevented locality-based analyses of Tunnel City Group *Dikelocephalus*, but this problem may be limited, because the specimens come from a much smaller geographic area than do samples from the St. Lawrence Formation (Hughes, 1993, fig. 2). Specimens from the Tunnel City Group are older than those

from the St. Lawrence Formation but stratigraphic relationships among the samples within the St. Lawrence Formation are not certain, except in those cases where collections were made from different beds at the same locality. Limited evidence suggests that the northern collections (Stillwater a and b) are older than that of Arcadia (A Aa), which is in turn older than collections from North Freedom (NF Beds 2 and 8) (Hughes, 1990).
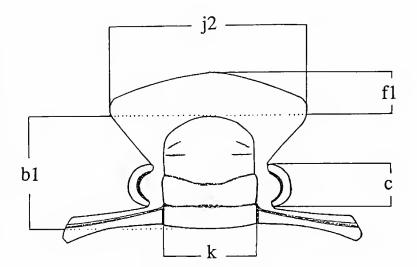
In an exploratory survey of morphological variation sclerites were placed in a Rost planvariograph (see Hughes and Rushton, 1990) and projected to a standard length. The outline of the projected sclerite was drawn onto tracing paper. Several traced images could then be superimposed, allowing swift visual assessment of differences. Some characters appeared static; others showed remarkable variability. Appropriate metric dimensions were then selected for morphometric analysis. Linear dimensions (Table 2; Figure 3) were measured using calipers, angular dimensions with a protractor. Because most specimens were too large to be measured using a microscope, measurements were taken normal to the surface being measured, rather than normal to a standardized plane (Shaw, 1957; Temple, 1975a). However, because many of the dimensions were taken from essentially planar surfaces, the disparity between surface-normal measurements and standard orientation measurements is insignificant.

Fossil preservation placed limitations on the range of characters available for study. Many sclerites are incomplete, preventing measurement of a full suite of characters. Labandeira and Hughes (1994) have shown that compaction has limited effect on statistical relationships of cranidia and pygidia of *Dikelocephalus,* provided that markedly distorted specimens are first removed from the data set. This may be because compaction does not result in marked lateral expansion (Briggs and Williams, 1981; Hughes, 1993), and hence has little effect on the measurements used in these analyses. This interpretation is supported by the observation (see below) that the strongest correlations in *Dikelocephalus* are between those metric dimensions most likely to be affected by compaction (i.e., orthogonal dimensions on arched surfaces). Furthermore, although many specimens included in these analyses have undergone compaction, the degree of compaction appears to be approximately similar in all specimens.

Free cheeks, thoracic segments, and ventral sclerites were excluded from the morphometric study. The curved shape of free cheeks limits the number of homologous points that can used in metric analysis. Free cheeks were also particularly prone to shape distortion during flattening due to their convexity (Hughes, 1993, pl. 5: figs. 4, 5), and such distortion has been shown to be the main cause for the variation in their shape (Labandeira, 1983). Isolated thoracic segments were excluded from the analysis because complete specimens show that segment morphology varies gradually along the thorax (see below), making it impossible to ascertain the original position of any disarticulated segment.

TABLE 2.—Symbols used for sclerite dimensions (after Shaw, 1956, 1957; Temple, 1975a).

Character	Abbreviation
Frontal area length (sag)	f1
Frontal area width (tr)	j2
Occipital–glabellar length (sag)	b1
Occipital lobe width (tr)	k
Palpebral lobe length (exsag)	c
Intra-articulating pygidial length (sag)	z1
Intra-articulating pygidial spine length (exsag)	z5
Pygidium axial length (sag)	y1
Maximum pygidial width (tr)	w
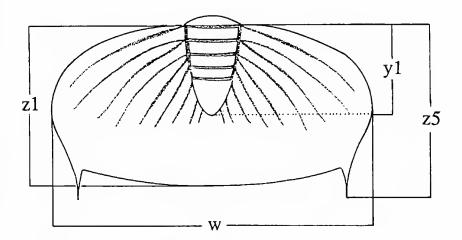
FIGURE 3.—Linear dimensions measured on cranidia and pygidia of *Dikelocephalus.* Abbreviations used for sclerite dimensions follow Shaw (1956, 1957) and Temple (1975a). For explanation see Table 2.

STATISTICS

The Pearson product-moment correlation coefficient and the reduced major axis were calculated in the analyses of nominal and ordinal characters. The product-moment correlation coefficient (r) measures the degree of association between two variables by assessing the extent to which two variables covary through growth. Comparison of the correlation coefficients of one variable with others allows assessment of the relative variability of that character.

Reduced major axis (RMA) is a form of regression analysis that describes the relationship between two characters during growth. It specifies the initial growth index (b) which is the relationship of the two variables at the start of growth, and the growth ratio (a) which is the ratio between the growth rates of the two variables (Imbrie, 1956). The reduced major axis line is calculated as the line that minimizes the sum of the products of the two variables (Rayner, 1985:425). This technique was used because it gives equal weight to each variable when calculating the best fit line, rather than assuming that one variable is dependant on the other as in conventional regression analysis (Imbrie, 1956). If the ratio between two dimensions of an organism does not change during ontogeny then growth is isometric. If the ratio changes, then growth is allometric (Gould, 1966; Raup and Stanley, 1985).

Reduced major axis analysis can be used to assess whether or not the growth relationships of a pair of characters are similar in different populations or taxa. It has been used in many studies of trilobites (e.g., Selwood, 1966; Pabian and Fagerstrom, 1968, 1972; Eldredge, 1972; Engel and Morris, 1989) and describes the growth trajectory (Eldredge, 1972) within a population, allowing a series of trajectories from different populations to be compared. In this study the reduced major axes of different collections were compared at the 95% significance level using the method of Imbrie (1956) and tests for isometry were computed using equations and tables given by Hayami and Matsukuma (1970). Statistically significant differences do not in themselves necessarily imply taxonomic differences (e.g., Sheldon, 1987). There are examples of statistically significant differences between populations in sclerite dimensions of some living arthropod species, (e.g., *Limulus polyphemus* Linnaeus: Riska, 1981 and references therein). If species are defined as basal differentiated taxa each must be characterized by unique combination of character states. Statistically significant differences between populations may be considered unique only if they define mutually exclusive groups the ranges of which do not overlap.

Intracollection variation can be assessed by the spread of variation about the generalized growth trend (i.e., reduced major axis). The coefficient of relative dispersion is a measure of this variation and expresses, as a percentage, the amount of shape variation as a proportion of the average shape within the sample (Imbrie, 1956).

Analysis of Nominal and Ordinal Characters

CRANIDIUM

ANTERIOR BORDER.—A swollen anterior border is common in many specimens of *Dikelocephalus* from the northern Mississippi Valley. One of Owen's syntype cranidia from Stillwater, Minnesota (SWa) (Owen, 1852, table 1, fig. 1), shows the development of an anterior border (Plate 11: Figure 17; Labandeira and Hughes, 1994, pl. 1: fig. 1) and many specimens from laminated sandstones show the development of an upturned or inflated anterior border (Plate 11: Figures 6, 7; Labandeira and Hughes, 1994, pl. 1: figs. 4–6). However, not all specimens preserved with the original relief possess a raised border (Hughes, 1993, pl. 2: figs. 3, 4) and the variation of the cranidial anterior margin is striking. The raised border can often be recognized within collections from heterolithic facies (Hughes, 1990). These fine-grained lithologies also commonly preserve terrace lines that run transversely along the anterior border (Plate 2: Figure 3, Plate 3: Figures 2–4, Plate 6: Figure 2; Hughes, 1993, pl. 4: figs. 6–8).

The variable nature of the anterior border was studied using collections from four localities (NF2, NF8, A Aa, and SWb) from heterolithic facies and one collection from the laminated sandstones of the Tunnel City Group (FG). Within each of these collections there was a variety of forms, some possessing an anterior border, others without. Variation in border morphology was not linked to other features indicative of flattening, such as glabellar relief.

In each of the collections the specimens with relatively long (sag.) frontal areas were those that also possessed an anterior border (Plate 2: Figure 3, Plate 3: Figures 2–4, Plate 4: Figure 4, Plate 6: Figures 6, 8–11, Plate 9: Figures 1–5, 7–11). This suggests that the presence or absence of the border is related to the position of the facial suture. In forms with long frontal areas the anterior of the cranidium probably extended to the anterior margin of the cephalon (as in the complete cephalon illustrated in Plate 1: Figure 1). This is supported by the observation that in many fused free cheeks the facial suture follows the anterior margin of the cephalon (Plate 2: Figure 4, Plate 3: Figures 7, 8; Hughes, 1993, pl. 4: fig. 2). However, in some individuals the anterior section of the facial suture is not marginal, but crosses the dorsal surface at some distance from the cephalic margin. In such cases the anterior of the cranidium is described as "retracted" from the anterior margin of the cephalon (Plate 5: Figure 2; Labandeira and Hughes, 1994, pl. 1: fig. 9). The extent of retraction is variable, but there is no relationship between cephalic size and either extent of retraction or the presence or absence of a raised anterior border (cf., Ludvigsen and Tuffnell, 1983, for *Triarthrus*). If marginal and retracted conditions characterize distinct morphs, this should be reflected in the results of statistical analyses of the frontal area length. However, this condidtion is not reflected in the analytic results (below); within-collection variation in the anterior border dimensions is continuous.

Some localities within the heterolithic facies are characterized by cranidia with a more strongly developed anterior border furrow than is usually found within this facies. They do not appear to have suffered less flattening than specimens from other localities. Specimens from LaGrange Mountain (RWa) consistently show a marked anterior border furrow, often with associated pits and caeca developed across the frontal area (Hughes, 1993, pl. 4: figs. 6–8, pl. 5: fig. 6; see below). Specimens from Arcadia Bed 18 (A Aa; Plate 3: Figures 2–4)

also show an anterior border furrow in all but the largest specimens, in which it may have been obliterated during compaction (Hughes, 1993). Specimens from these localities have relatively long (sag.) frontal areas (the importance of this locality-based variation is discussed below). There are no grounds for considering the anterior border a species-specific character. Despite its variable condition, however, it has long been considered to be of taxonomic significance in *Dikelocephalus*. The development of the anterior border furrow and inflated border in *Dikelocephalus minnesotensis* was first recognized by Hall (1863), and illustrated with a single fragmented cranidium showing a swollen border (Hall, 1863, pl. 9: fig. 12). This specimen, from the *Saukia* fauna heterolithic beds at LaGrange Mountain (RWa), has a markedly convex anterior brim with pits weakly developed in the anterior border furrow (Hughes, 1993, pl. 4: figs. 7, 8). Hall referred to this specimen as *D. minnesotensis* var. *limbatus*, commenting that "it may be imprudent to multiply specific designations for such remarkable forms as the *Dikelocephalus minnesotensis*" (Hall, 1863:141).

Walcott (1914, pl. 65: figs. 5–8) illustrated several specimens that he considered conspecific with *D. minnesotensis* var. *limbatus*. He assigned these to *Dikelocephalus ? limbatus* Hall. On morphological and stratigraphic grounds the association of these specimens seems unlikely and the validity of Walcott's species is therefore dubious. Walcott's material is all significantly older than Hall's specimen. Most of these specimens have since been reassigned to different species or genera. One pygidium (Walcott, 1914, pl. 65: fig. 8), from the Mazomanie Formation, near Baraboo, was transferred to *Briscoia winchelli* (Resser, 1942). The cranidium and pygidium illustrated by Walcott (1914, pl. 65: figs. 6, 7) from the laminated sand subfacies at Osceola, Wisconsin, belong to the *Osceolia osceola* Subzone and were assigned to *Dikelocephalus thwaitesi* by Ulrich and Resser (1930). A cranidium (Walcott, 1914, pl. 65: fig. 5) from the *Osceolia osceola* Subzone heterolithic facies at Osceola is here considered to belong to *Osceolia*.

An inflated border area was used in the diagnoses of three species of *Dikelocephalus: D. marginatus, D. norwalkensis,* and *D. thwaitesi* (Ulrich and Resser, 1930). These species, in amended form, were maintained by Raasch (1951). *Dikelocephalus freeburgensis* Kurtz (Bell, Feniak, and Kurtz, 1952) from the Reno Member also shows an anterior border furrow (Plate 9: Figures 3–5). *Dikelocephalus marginatus* came from heterolithic facies at LaGrange Mountain (RWa). This locality has been discussed above. *Dikelocephalus thwaitesi* and *D. norwalkensis* came from sandstone facies and are preserved with putative original relief. All other species based on cranidia by Ulrich and Resser (1930) came from heterolithic facies, where compaction has reduced the prominence of the anterior border. As shown above, the development of the anterior border is variable within collections and can not be considered significant in the diagnoses of these species.

Some *Dikelocephalus* specimens from outside the northern Mississippi Valley also show variable development of the anterior border. A specimen that is preserved in original relief from the Snowy Range Formation, Montana (Grant, 1965, pl. 15: fig. 1), clearly shows an anterior border furrow and raised border. Specimens from the Rocky Mountains of Alberta (Westrop, 1986, pl. 3: figs. 1–3) lack an anterior border furrow, although the border of the largest specimen (Westrop, 1986, pl. 3: fig. 2), which is slightly compacted, appears to be slightly inflated. These specimens support the suggestion of locality-based variation in the development of the anterior border.

The cranidium from the Upper Franconian of the Arbuckle Mountains, Oklahoma, assigned to *Dikelocephalus* species 1 by Stitt (1971, pl. 3: fig. 20) also possesses a deep anterior border furrow that widens (sag.) adaxially on its short (sag.) frontal area. In addition to the unusual abaxial widening of the anterior border furrow, the glabella is more elongate than in *Dikelocephalus*. This specimen is here considered to belong a different genus.

Lochman (1959) stated that the absence of an anterior border furrow in *Dikelocephalus* was a useful character for distinguishing this genus from *Briscoia*. She also considered the possession of a pair of posterolateral pygidial spines to be characteristic of *Dikelocephalus*. It is not clear what she regarded as the taxonomic status of described *Dikelocephalus* species that possess both an anterior border and pygidial spines.

Westrop (1986) argued that specimens of *Briscoia dalyi* (Walcott) show progressive effacement of the anterior border furrow through holaspid ontogeny, making the absence of a border furrow unreliable for use in distinguishing between *Briscoia* and *Dikelocephalus*. Westrop's (1986, pl. 2: figs. 1, 2, 5–8, 10) illustrations show a clear size-related trend from small specimens with firmly impressed anterior border furrows to larger specimens with very shallow furrows; this may reflect ontogenetic control. The variability in the anterior border of *Dikelocephalus*, on the other hand, appears to be size-independent.

CAECA.—Caeca are not prominent in *Dikelocephalus*. Where obvious, they are usually found in association with a well-developed anterior border furrow. Specimens from La-Grange Mountain, Redwing (RWa), Minnesota, may show the development of irregular caeca, together with pits in the anterior border furrow in small individuals (Hughes, 1993, pl. 4: figs. 6–8, pl. 5: fig. 6). The spacing between pits is highly variable, even within individual cranidia. Similar caeca are seen in specimens from Galesville and Stoddard, Wisconsin, and are about 0.5 to 2.0 mm wide. Caeca are probably present in many other specimens (e.g., Plate 3: Figures 3, 4, Plate 10: Figures 14, 15, Plate 11: Figures 1, 2) but are less distinct and cannot be identified with certainty. Caecal development is variable within collections.

The original description of *Dikelocephalus minnesotensis* var. *limbatus* (Hall, 1863:141) mentioned "a few wrinkled striae, directed toward the glabella" that originated in the

anterior border furrow (Hughes, 1993, pl. 4: figs. 6, 7). These structures have also been reported in *Briscoia sinclairensis* Walcott (see Walcott, 1924, pl. 20: fig. 2) and in *Briscoia* specimens from central Texas (see Bell and Ellinwood, 1962, pl. 52: fig. 5) but not in any other dikelocephalid. Caeca appear in other libristomate trilobites (see Fortey, 1974; Jell, 1978; Babcock, in press, for examples) and are considered to reflect the morphology of soft parts underneath the dorsal surface. The development of the pits and caeca in *Dikelocephalus* appears to be much less regular than in most other primitive libristomates (Fortey, 1974; Jell, 1978). The absence of caeca in most specimens does not necessarily imply that the soft parts that they represented were absent in other *Dikelocephalus*.

EYE RIDGES.—Faint eye ridges are present in many specimens of *Dikelocephalus* from all localities studied (Plate 2: Figure 3, Plate 3: Figure 6, Plate 6: Figures 7, 8). They are particularly obvious in larger specimens, in which the palpebral lobes are relatively small, and where the preoccipital fixed cheek is wider (see below). In some specimens they continue into a slight swelling of the interocular fixed cheek opposite the midpoint of the palpebral lobe (Plate 4: Figures 8, 9). The occurrence of the eye ridges is gradational and their morphology is variable within collections.

The presence of the eye ridge in *D. minnesotensis* was discussed by Ulrich and Resser (1930) but was not used as a diagnostic feature in their species designations. Lochman (1959) noted that the eye ridges in *Dikelocephalus* are faint.

EYE POSITION.—The position of the palpebral lobe varies within *Dikelocephalus*. In specimens from the St. Lawrence Formation the eye is centered opposite or slightly anterior of the midpoint of the first glabellar lobe (e.g., Plate 3: Figures 1–7, Plate 6: Figures 1–14). Some specimens from the Tunnel City Group have the eye centered opposite, or just posterior of, the confluence of the first glabella furrow with the axial furrow (Plate 9: Figures 1–5, 8–11). Other specimens have it in the same position as in St. Lawrence Formation *Dikelocephalus* (Plate 9: Figure 15). There is continuous gradation between these two conditions within collections from both the Tunnel City Group and the St. Lawrence Formation, suggesting that eye position is not a species-diagnostic character.

The position of the eye lobe has been considered to be of taxonomic importance for distinguishing *Briscoia* and *Dikelocephalus* (Westrop, 1986). In the Tunnel City Group specimens the eye is centered in the same position as in *Briscoia septentrionalis* Kobayashi (see Palmer, 1968) and *Briscoia angustilimba* Westrop, 1986. The position of the eye, therefore, does not seem to be genera specific in the dikelocephalids.

ORNAMENTATION.—Development of surface ornamentation on the frontal and posterolateral borders is variable. In most cranidia transverse terrace lines are present on the frontal area, just anterior of the glabella (Plate 3: Figures 2–4, Plate 4: Figure 4, Plate 6: Figures 1–14). The occurrence of these terrace lines is independent of size (Plate 6: Figures 1–14). They are continuations of those developed on the free cheeks

and tend to become wavy and inosculate towards the ocular region (Plate 6: Figure 7). Some specimens show terrace lines on the posterolateral border, in addition to two transverse striations that are developed adaxially on the spatulate posterolateral border.

These features are only preserved in specimens from the fine-grained heterolithic facies, and their absence from specimens preserved in sandstones is likely due to preservational factors.

GLABELLA

Glabellar characters have been considered to be especially important in trilobite taxonomy (Stubblefield, 1936; Fortey and Owens, 1979; Whittington, 1981; McNamara, 1986; Fortey and Chatterton, 1988) and Ulrich and Resser (1930:18) commonly used the shape, contour, and furrows of the glabella in the discrimination of *Dikelocephalus* species. Some aspects of glabellar shape and ornament are described in this section, whereas others are treated bivariately. Variation in relief of the glabella is commonly the result of compaction (Hughes, 1993), but well-preserved specimens show variation even between specimens from individual localities (Plate 6: Figures 7, 9, 11–14).

ANTERIOR MARGIN.—Well-preserved material shows that the shape of the anterior margin of the glabella varies slightly, from well-rounded to more truncate, among specimens from the same localities (e.g., Plate 4: Figures 4, 5, Plate 6: Figures 2, 6–11, 13). However, this variation is not obviously related to either size or locality, and is not linked to that of any other character.

Ulrich and Resser (1930) often commented on the shape of the anterior glabella in their species designations. They considered the axial furrow in front of the glabella in Owen's (1852) syntype of *D. minnesotensis* to be "decidedly straightened in the middle" (Ulrich and Resser, 1930:21) and used this character to distinguish *D. minnesotensis* from their *D. hotchkissi* in which "the anterior part of the outline [of the glabella] is more rounded" (Ulrich and Resser, 1930:23). Re-examination of Owen's original material (Plate 11: Figure 17; Labandeira and Hughes, 1994, pl. 1: fig. 1) shows that the specimen has been subjected to compaction-related distortion, which straightened the anterior margin of the glabella. The orientation of the specimen and retouching of photographs by Ulrich and Resser (1930, pl. 1: fig. 6) also over emphasized the straightness of the margin.

LATERAL GLABELLAR FURROWS.—All specimens of *Dikelocephalus* show at least one pair of glabella furrows (S1). The second pair (S2) is absent only in specimens showing considerable compaction (Plate 3: Figures 5, 6) and was probably present in all specimens. There are three important ways in which the glabella furrows vary within *Dikelocephalus*: (1) presence of the third glabellar furrow (S3); (2)

confluence of the first and second glabellar furrows (S1 and S2) with the axial furrow: and (3) angular relationship of S1 and S2 furrows to the sagittal axis.

S3 is most common in small specimens (Plate 2: Figures 1–3, Plate 3: Figures 1–4, Plate 4: Figure 4, Plate 6: Figures 1–7), but may also be present in large specimens (Plate 6: Figure 11). Owen's (1852) original, discussed by Ulrich and Resser (1930), shows S3 and is above average size (b1 = 4 cm) (Plate 11: Figure 17; Labandeira and Hughes, 1994, pl 1: fig. 1). Many of the largest specimens, however, show only faint S3 furrows and in many cases S3 furrows are absent (Plate 2: Figure 8, Plate 4: Figure 9, Plate 6: Figures 13, 14, Plate 7: Figure 1).

The presence of a third pair of glabellar furrows in Owen's syntype cranidium of *Dikelocephalus minnesotensis* was noted by Ulrich and Resser (1930:21-22) who observed that "the anterior pair is indicated, sometimes only on one side, by very obscure impressions that appear to turn forward rather than [run] directly across and do not start at the dorsal [i.e., axial] furrow." Inspite of their recognition of variation in S3, Ulrich and Resser did not place any taxonomic importance on the occurrence of these furrows.

Labandeira (1983:164-165) commented that the number of occipital and lateral glabellar furrows is variable, ranging from two in some large specimens to four (or five?) in smaller specimens. Of these the S3 furrows are usually faint, incomplete and highly variable in their angular relationship with the axial furrow. New material confirms Labandeira's (1983) suggestion that the number of furrows is size-related. However, Labandeira's interpretation of five cephalic axial furrows in some of the smaller specimens is questionable. A variety of minor intercalated furrows are present in addition to the occipital and glabellar furrows in a few specimens, but these are not considered homologous with the major lateral glabellar furrows and are discussed separately (see below).

Within individual collections of *Dikelocephalus* some specimens show confluence of S1 and S2 with the axial furrow, and others do not (Plate 2: Figures 1–3, 6–8). This pattern of variation is apparently unrelated to size or to locality.

The angular relationship of the medial portions of S1, S2, and S3 to the sagittal axis has been examined in detail by Labandeira and Hughes (1994, fig. 2), who concluded that variation in this character was continuous. Analysis using the planvariograph showed no consistent size-related or locality-based variation in this character (e.g., Plate 6: Figures 1–14), thus confirming Labandeira and Hughes' conclusion.

Many specimens show additional furrows, which are termed intercalated furrows (e.g., Hughes, 1993, pl. 5: figs. 6, 7). Although they are sometimes faintly present in material retaining original relief, intercalated furrows are particularly common in slightly compressed specimens (Hughes, 1993, pl. 5: fig. 7). Slight compression may actually enhance these features (see Henningsmoen, 1960, for examples of compres-

sion-enhancement of internal features). There are no obvious controls on their occurrence other than compression. Minor "furrows" developed within the lateral glabellar lobes are present in a wide variety of trilobites (e.g., the ceratopygid *Cermatops discoidalis* (Salter): Hughes and Rushton, 1990; the dikelocephalid *Briscoia platyfrons* Ulrich and Resser: Walcott, 1914, pl. 65: fig. 4).

MEDIAN OCCIPITAL TUBERCLE.—A small tubercle is present on the occipital lobe of just more than half the *Dikelocephalus* cranidia studied from four localities in the heterolithic facies (Ferguson's collection from Stillwater (SWb), Arcadia Bed 18 (AAa), North Freedom Bed 2 (NF2), and North Freedom Bed 8 (NF8)) (Figure 4). The occurrence of the median tubercle is not size-related, as it is present in approximately half the samples in each cranidial size class (Figure 5). The tubercle apparently maintains the same size relative to the glabellar length throughout growth (Plate 2: Figures 1–3, 6, 7, Plate 3: Figures 1–5, Plate 6: Figures 1–14, Plate 10: Figures 14, 15).

Interpretation of the occurrence of the median tubercle is complicated by the tubercle's morphological variability. In some specimens it is prominent (Plate 6: Figures 8, 11); in others it has low relief and is difficult to distinguish from glabellar pustulation (Plate 6: Figure 3). The absence of the tubercle is not due to taphonomic factors because some well-preserved specimens lack any indication of a median tubercle (Plate 6: Figures 4, 9). As the median tubercle is present in approximately half the specimens and is size-independent, it may represent a dimorphic character. Dimorphism in sclerite characters has been reported in many trilobites (e.g., Selwood and Burton, 1969; Hu, 1971; Campbell, 1977) and is commonly sexually-related in modern arthropods (Hartnoll, 1982). However, the prominence of the tubercle appears to vary continuously and this variation is not linked to that of any other character.

Ulrich and Resser's (1930:33) discussion of *D. oweni* includes reference to "the usual median tubercle." It seems that
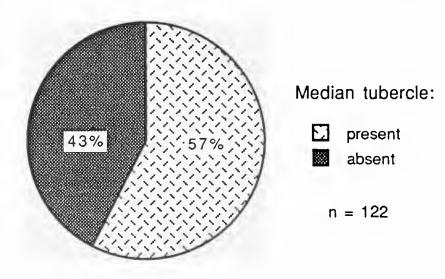

FIGURE 4.—Pie diagram showing percentage occurrence of median tubercle in *Dikelocephalus* cranidia from four localities in the St. Lawrence Formation. Localities are Stillwater (SWb), Arcadia Bed 18 (AAa), North Freedom Bed 2 (NF2), and North Freedom Bed 8 (NF8).
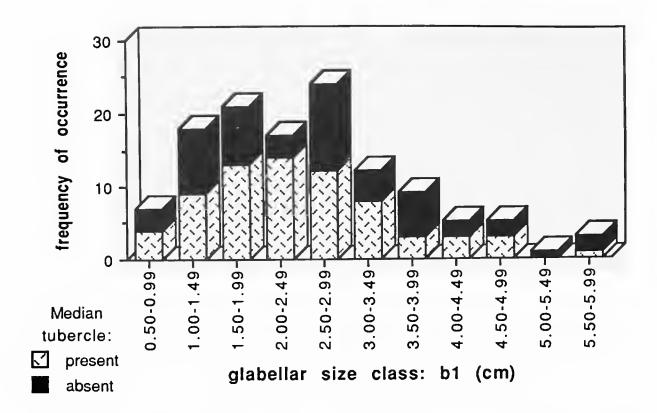
FIGURE 5.—Bar chart showing relationship between occurrence of median tubercle and glabellar size from pooled sample of *Dikelocephalus* cranidia from four localities in the St. Lawrence Formation; n = 122. Localities are Stillwater (SWb), Arcadia Bed 18 (A Aa), North Freedom Bed 2 (NF2), and North Freedom Bed 8 (NF8).
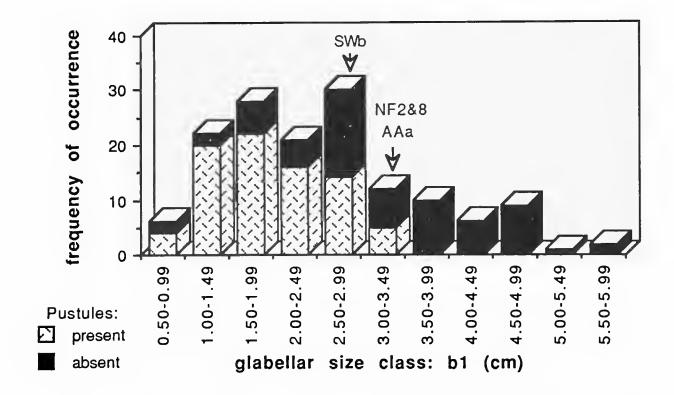
FIGURE 6.—Bar chart showing relationship between occurrence of glabellar pustulation and size. Arrows mark the size class of the largest pustulated cranidium of *Dikelocephalus* at each of four localities in the St. Lawrence Formation; n = 147. Localities are Stillwater (SWb), Arcadia Bed 18 (A Aa), North Freedom Bed 2 (NF2), and North Freedom Bed 8 (NF8).

they thought it was present in all *Dikelocephalus,* as this feature was not discussed elsewhere in their monograph.

ORNAMENTATION.—Most small cranidia of *Dikelocephalus* have pustules developed on the glabella; all large cranidia lack them. The restriction of pustules to smaller forms is unlikely to

be a taphonomic artifact, because many large cranidia that lack pustules show excellent preservation of other surface ornament (Plate 6: Figure 11, 13). Populations from single bedding planes show that pustulation is absent in all specimens with an occipital glabellar length greater than 3.5 cm (Figure 6). The

absence of pustules in some small individuals may be due to taphonomic factors. In very small cranidia the pustules are so tiny that the sediment grain size of even the fine-grained units is too coarse to permit their preservation. All small specimens that show surface ornamentation on other parts of the cranidium also show pustules. It is therefore likely that all small *Dikelocephalus* from the northern Mississippi Valley were pustulated in life.

Examination of collections from single bedding planes reveals no clear division between the pustulated and non-pustulated forms. Pustules in *Dikelocephalus* are distinctive in small cranidia but in larger specimens they are less densely concentrated and of lower relief (Plate 6: Figures 1-10). This transition forms a gradual and continuous trend toward total loss of pustules at large size. As glabellar size increases pustules become restricted to axial regions (Plate 6: Figures 9, 10). These observations indicate that pustule development was ontogenetically controlled and that all individuals eventually lost their pustules during ontogeny. There is no evidence of separate pustulated and non-pustulated morphs (as are reported in *Dechenella,* by Selwood, 1965, or *Paciphacops logani* (Hall), by Campbell, 1977). The size of cranidia at which the last remnant of pustulation is detectable is approximately the same in all localities (Figure 3), suggesting that this control was locality-independent. A similar relationship was present throughout all the collections examined from the heterolithic facies. Although taphonomic factors prevent assessment of the maximum size of individuals living at each locality, it seems probable that the size range of *Dikelocephalus* was locally variable, as is common in other trilobite species (Sheldon, 1988). The observation that pustules become obsolete at approximately the same size at all localities suggests that there may have been an adaptive reason for pustule loss at a particular size.

To explore the growth parameters of pustulation the diameters of five pustules were measured on 34 cranidia from Stillwater (SWb), Arcadia (A Aa), and North Freedom (NF2, NF8). These values were averaged and then plotted against occipital-glabellar length (b1). Results show a strong correlation between these variables ($r = 0.880$) (Figure 7). The reduced major axis coefficient (0.883) is not significantly different from isometry at the 95% confidence level, but a plot of the ratio of pustule diameter to glabellar length against occipital-glabellar length (Figure 8) suggests a slight decrease in the relative size of the pustules in larger cranidia.

Most small cranidia from outside the northern Mississippi Valley, preserved in fine-grained limestones, do not have pustules (Plate 11: Figures 11, 15; Grant, 1965, pl. 13: fig. 1; Westrop, 1986, pl. 3: fig. 1). All surface ornament is lacking in these specimens and the significance of the absence of pustulation is difficult to evaluate, although other trilobite species from the same lithologies display surface ornament. A single cranidium preserved in limestone from Hudson Creek,

Texas (b1 = 0.8 cm, Plate 11: Figure 14), does show small pustules, indicating that at least some pustulated individuals lived outside the northern Mississippi Valley. Hence biological variation in *Dikelocephalus* ornament occurs throughout its geographic range.

Glabellar ornamentation was used by Ulrich and Resser (1930) to designate two small species, *D. granosus* and *D. barretti*. The results above indicate that pustulation is not an appropriate character for specific designation in *Dikelocephalus* and these species are therefore considered to be invalid. The fact that few specimens illustrated by Ulrich and Resser (1930) show pustulation reflects their bias toward selecting larger specimens for illustration, in which pustulation is consistently absent.

Raasch (1951) suggested that pustulation was common among small cranidia of *Dikelocephalus* in his *Saukia sublonga* faunal unit of the heterolithic facies and reported that pustulation persisted into medium-sized forms in the underlying *Saukia subrecta* unit. Raasch (1951) correctly implied that pustulation was ontogenetically controlled but thought that its development varied through time. The results above do not support the conclusion that there was stratigraphic control of pustule development. Collections analyzed here came from throughout the heterolithic facies, but all show pustule loss at a similar size.

Labandeira (1983) noted that pustulation was not present on all small specimens, and suggested that pustule variation should be classed as ecophenotypic rather than ontogenetic in origin, although the data were ambiguous. Labandeira's observation was based on Ulrich and Resser's material which included disproportionately few small specimens. This fact, coupled with the abraded condition of much of this material, lead to under-representation of pustule occurrence in the type suite.

FREE CHEEKS

MEDIAN SUTURE.—A striking morphological variation within *Dikelocephalus* is the intermittent presence of the median connective suture, which joins the dorsal facial suture with the hypostomal suture. The median suture was considered synapomorphic for the Order Asaphida (Fortey, 1990) by Fortey and Chatterton (1988), who demonstrated loss of the structure in several groups (see below). Complete cephala of *Dikelocephalus* possessing a median suture are rare. Ulrich and Resser (1930, pl. 10: fig. 2) figured a specimen in which the original orientation of the free cheeks had been disturbed. In this specimen a median suture is present (Labandeira and Hughes, 1994, pl. 1: fig. 8). A median suture may be present in an extremely large pair of free cheeks from Muscoda, Wisconsin (Hughes, 1993, pl. 4: fig. 4). However, this structure could be a crack, as its course is slightly irregular. Many isolated free cheeks show a sharp truncation of the doublure along the sagittal axis, which is likely to represent a median suture (Plate

FIGURE 7.—Bivariate scatterplot showing relationship between average pustule size (mean of five pustules measured on each cranidium) and occipital-glabellar length in *Dikelocephalus* from four localities in the St. Lawrence Formation; n = 34. Localities are Stillwater (SWb), Arcadia Bed 18 (A Aa), North Freedom Bed 2 (NF2), and North Freedom Bed 8 (NF8).
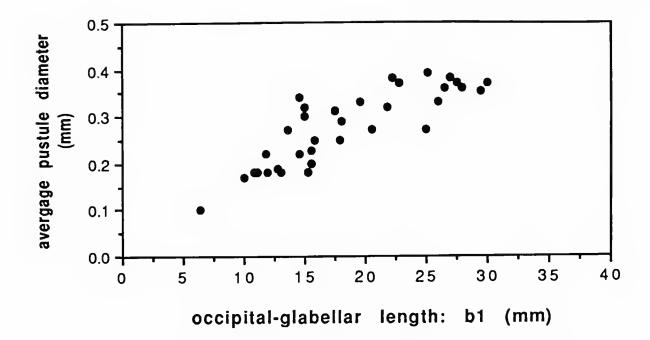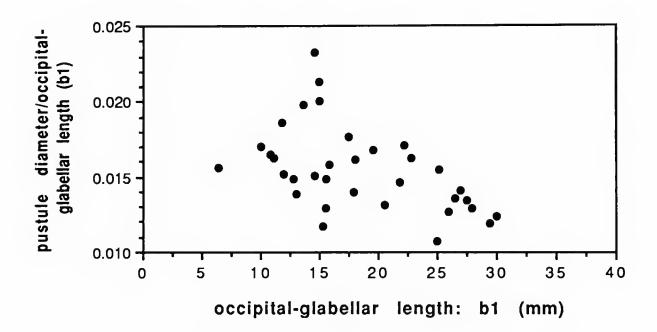

FIGURE 8.—Bivariate scatterplot of ratio of average pustule size divided by occipital-glabellar length plotted against occipital-glabellar length for same data set as in Figure 7. Note the general decrease in relative pustule size.

3: Figure 7, Plate 5: Figure 1, Plate 7: Figure 5; Labandeira and Hughes, 1994, pl. 1: fig. 10). This suggests that a functional median suture was commonly present in *Dikelocephalus*. However, there are also many specimens of fused free cheeks that lack evidence of a median suture (Plate 1: Figure 2, Plate 2: Figure 4, Plate 3: Figure 8, Plate 5: Figure 2). In these cases the doublure is continuous across the sagittal axis. There is little evidence of fused (i.e., non-functional) median sutures in *Dikelocephalus*. A lineation, which has not developed completely across the doublure, is present in one yoked pair of free cheeks from North Freedom Bed 2 (Hughes, 1993, pl. 4: fig. 2).

This is slightly irregular and may be a crack, rather than a partially fused median suture.

There is no obvious control on the presence or absence of the median suture. All collections studied from the St. Lawrence Formation include specimens that have and lack it. Its occurrence is not size-related (Plate 5: Figures 1, 2; Hughes, 1993, pl. 4: fig. 2). Ulrich and Resser (1930:42) suggested that specimens that possessed a median suture showed a facial suture that was "entirely dorsal, passing around the brim of the cephalon ... inside the [anterior] edge of the cephalon." New material disproves this. Some specimens, which clearly lacked

a median suture, had a marginal facial suture (Plate 2: Figure 4, Plate 2: Figure 8; Hughes, 1993, pl. 4: fig. 2). Others, which had the facial suture retracted, (see above) probably possessed a median suture (Plate 5: Figure 1). In fact, variation in the presence of the median suture is not related to variation in any other character in *Dikelocephalus* (Rasetti, 1952). Because there is no obvious pattern of occurrence, and because it is not obviously linked to variation in any other character, the presence of the median suture is not considered species diagnostic. It was not essential in the molting process of *Dikelocephalus* (see Hughes, 1993) and in some cases it appears to be only partially developed. Conjoined free cheeks are also present in *Dikelocephalus* from the Tunnel City Group.

The presence or absence of the median suture was used by Ulrich and Resser (1930) as a key character for distinguishing two groups within the genus: the *oweni* group, including *D. oweni* and *D. raaschi*, which possessed a median suture; and the *gracilis* group including *D. retrorsus*, *D. ovatus*, *D. granosus*, *D. gracilis*, and *D. subplanus*, which lacked the suture. Rasetti (1952:892) questioned the validity of a large number of *Dikelocephalus* species from the northern Mississippi Valley noting that "in other species of the genus, almost indistinguishable from [*Dikelocephalus retrorsus* and *D. subplanus*] in other characters, there is a median suture." The results of this analysis support Rasetti's (1952) view; no taxonomic significance can be attributed to the variable nature of the median suture.

The interpretation of variation in the presence of the median suture as an intraspecific variable is consistent with the pattern shown in *Isotelus gigas* DeKay (Henningsmoen, 1975; Jaanusson, 1975; Ludvigsen, 1979) and is also characteristic of other asaphide species (Ludvigsen, 1979). The loss of the median suture in some kainellids by the fusion of the free cheeks is recognized as a secondary condition in the Remopleuridacea (Fortey and Chatterton, 1988). It appears that fusion of the free cheeks was a common secondary condition in asaphide trilobites.

LATERAL BORDER.—A slight marginal swelling is present in many specimens of *Dikelocephalus* (Plate 3: Figure 7, Plate 7: Figure 7) and is often associated with a weakly impressed lateral border furrow and terrace ridges (Plate 2: Figures 10, 11). It marks the lateral extension of the anterior border. Even in specimens preserved with original relief it is never prominent (Plate 9: Figure 6; Hughes, 1993, pl. 1: fig. 2, pl. 5: figs. 4, 5). Variation in the marginal border of *Dikelocephalus* is slight and probably compaction-related. Ulrich and Resser (1930:18) stated that the presence of the marginal border (and associated lateral border furrow) was useful in the distinction of species, particularly in *D. norwalkensis*, which is preserved with its original relief in laminated sandstones, but also in *D. marginatus* from the heterolithic facies. A reexamination of this material (Labandeira and Hughes, 1994, pl. 1: fig. 10) suggested that a slightly raised rim is present in the syntypes of

D. marginatus but that it is no more prominent in these specimens than in others of Ulrich and Resser's species (e.g., *D. declivis*; Ulrich and Resser, 1930, pl. 15: fig. 9).

LENGTH OF GENAL SPINE.—The length of the genal spine is variable in *Dikelocephalus* (Plate 1: Figures 1, 2, Plate 5: Figure 1, Plate 7: Figure 5). It probably extended at least as far as the anterior of the pygidium in smaller specimens (Plate 1: Figures 1, 2). The entire length of the spine is rarely preserved so it has not been possible to draw conclusions on the nature of its variation.

Ulrich and Resser (1930) based some of their species designations on the inferred nature of the termination of the spine as interpreted from the morphology of its base. In the description of *D. ovatus* they stated that "the genal spines themselves are not completely preserved but what remains of them shows that they have broader bases and suggests that they are also shorter than in *D. gracilis*" (Ulrich and Resser 1930:45). In contrast, they suggested that *D. wisconsinensis* was characterized by the "great length of the genal spines" (Ulrich and Resser 1930:41). The present examination suggests that the supposed inverse relationship between the width of the spine at its base and its total length cannot be established conclusively. Although Labandeira (1983:139) did not include genal spine length in his morphometric analysis of Ulrich and Resser's type suite, he suggested that genal spines are more morphologically variable than glabellae.

ORNAMENTATION.—The number and form of dorsal terraces varies slightly between specimens within localities but is not size-related. Ridges tend to become inosculate and granular on the ocular platform. One specimen, preserved with original cuticle, shows granulations that are hexagonal (Hughes, 1993, pl. 1: fig. 2). The unique occurrence of such structures is attributed to the unusual preservation of the cuticle and is not considered taxonomically important.

HYPOSTOME (LABRUM)

The planvariograph method (see above) indicated that measurement of the hypostome was unlikely to provide information on growth controls within *Dikelocephalus*; morphometric analysis of the hypostome was restricted to measurements relating to the size of the maculae. Analysis of the type suite showed that the relative length and width of the hypostome remained constant through ontogeny (Labandeira and Hughes, 1994, fig. 8).

The median body shows some variation in convexity, but this is likely to be influenced partially by compaction. Large specimens frequently show cracks developed along the sagittal axis. The length/width ratio of the median body remained constant through growth but well-preserved specimens suggest that the median body may have become less convex during ontogeny (Plate 2: Figures 5, 9, Plate 7: Figures 9–12), supporting a similar observation made by Labandeira (1983).

The fine "thumb print" terracing evident on the median body

of many large hypostomes (Plate 3: Figure 9; Hughes, 1993, pl. 7: figs. 1, 2) was probably originally present in all specimens.

Maculae are more common in small specimens than in large ones (Figure 9; Labandeira and Hughes, 1994, pl. 1: fig. 11). Hypostomes from individual bedding plane collections show a trend toward effacement of maculae at large sizes (Plate 2: Figures 5, 9, Plate 5: Figures 3, 4) but sample sizes are too small be assessed statistically. As the largest specimens are often excellently preserved (Plate 7: Figure 11; Hughes, 1993, pl. 7: figs. 1, 2) the progressive effacement of maculae is not merely due to compaction. Not all small specimens show well-developed maculae (Figure 9), possibly indicating that the pattern of variation was not controlled by size alone. Investigation of possible locality-related influences on maculae development is prohibited by small sample sizes (see Hughes, 1993). Maculae apparently grew at a rate directly proportional to glabellar size, but became gradually effaced (i.e., less prominent) through holaspid ontogeny.

Ulrich and Resser (1930) were reluctant to base species designations on the basis of hypostomal characters alone, although they thought that the prominence of maculae varied between species. Labandeira (1983) and Labandeira and Hughes (1994) considered macular variation to be "intraspecific," a conclusion supported by this study.

THORAX

NUMBER OF THORACIC SEGMENTS.—The smallest and largest articulated specimens show nine thoracic segments, but their thoraxes are not complete (Plate 1: Figures 1, 2). In the largest specimen the pygidium is telescoped over part of the thorax (Plate 1: Figure 1) and it is not possible to determine whether other segments are hidden beneath it. The smallest specimen is rather poorly preserved and lacks the cranidium (Plate 1: Figure 2). An inverted segment lies within the cephalic body cavity and originally may have been part of this individual, lying at the anterior of the thorax. There were probably at least ten thoracic segments during life. In both these specimens the pygidium lies slightly oblique to the cephalon, suggesting that they may represent molts rather than dead individuals (see Henningsmoen, 1975). A third specimen has twelve segments, and although the cephalon and pygidium are poorly preserved, the thorax appears to be complete (Plate 1: Figure 3).

Some, if not all, *Dikelocephalus* had twelve thoracic segments in the holaspid stage. The difference in segment numbers between the three specimens could be accounted for by taphonomic factors alone. However, it seems unlikely that as many as three segments are missing from the largest specimen (Plate 1: Figure 1) and there may be additional biological reasons for the variation in segment number. The variation is unlikely to be growth-related, as the specimen showing the smallest number of segments is the largest of the three. Intraspecific variation in the number of thoracic segments is not uncommon in trilobites. The thorax of adult *Paradoxides davidis brevispinus* Bergström and Levi-Setti contains 19 to 21 segments and other subspecies show similar variation in segment number (Bergström and Levi-Setti, 1978). Within the ptychoparioid species *Elrathia kingii* (Meek) the adult thorax contains 10 to 13 segments (Bright, 1959).
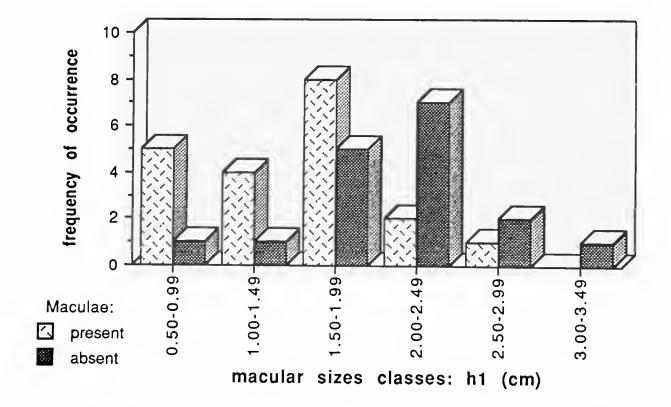

FIGURE 9.—Bar chart showing relationship between occurrence of maculae and the length of the hypostome in *Dikelocephalus* from four localities in the St. Lawrence Formation; n = 39. Localities are Stillwater (SWb), Arcadia Bed 18 (A Aa), North Freedom Bed 2 (NF2), and North Freedom Bed 8 (NF8).

ANTERIOR MARGIN OF THORACIC SEGMENTS.—Study of new and more complete material shows that the shape and furrows of the thoracic segments varied markedly along the thorax (Plate 1: Figures 1-3). Ulrich and Resser (1930) considered the characteristics of the thoracic segments to be important for identifying *D. orbiculatus*. The anterior margin of an isolated segment attributed to *D. orbiculatus* shows a uniform curve (Ulrich and Resser, 1930, pl. 4: fig. 4), which they considered to be diagnostic of this species. However, most segments near the posterior of the thorax show this uniform curve and, as it is impossible to determine the position of this isolated segment in the thorax. The use of curvature in taxonomic discrimination cannot be justified.

ORNAMENTATION.—The petaloid ornamentation of the anterior facets of thoracic pleurae varies in appearance, probably due to preservational control. A faint median tubercle is evident on the axial ring of a small number of specimens (Plate 2: Figure 12). Granular pustules are developed on adaxial portions of the opisthopleurae and on the axial ring of some smaller segments (Plate 3: Figures 10, 11, Plate 5: Figure 5, Plate 7: Figure 13). These pustules are absent in larger specimens (Hughes, 1993, pl. 4: fig. 5), probably reflecting an ontogenetic control.

PYGIDIUM

AXIAL FURROWS.—Four axial rings and a terminal piece are present in all *Dikelocephalus* except those showing teratologies (e.g., Hughes, 1993, pl. 7: fig. 7). The furrow defining the posterior margin of the fourth ring is variably incised but prominent (Plate 5: Figures 6, 8, 10, 11). There are no obvious size or locality controls on its prominence. A few specimens show up to two weak and incomplete furrows on the terminal piece (Plate 5: Figure 11; Ulrich and Resser, 1930; Lochman, 1959). They are similar in appearance to those described in species of *Centropleura* (Öpik, 1961, pl. 8; Babcock, in press, figs. 18, 20). These features are too rare to permit any assessment of likely controls on their occurrence. An anteriorly facing ridge arches from the posterior border of the first two axial rings in many specimens (Plate 5: Figures 9, 10, Plate 8: Figure 8). This structure is probably an incompletely developed articulating half ring, as in *Ceraurus* (Whittington, 1959).

TERMINATION OF THE AXIS.—The shape of the terminal piece is somewhat variable within *Dikelocephalus*. In this analysis it was assigned to one of three character states: smooth (e.g., Plate 8: Figures 11, 12), intermediate (e.g., Plate 8: Figures 5, 6), or sharp (e.g., Plate 8: Figure 1). The boundaries between these states were arbitrary, reflecting a morphological continuum. Results suggest that termination states are randomly distributed both with respect to locality and to pygidial size (Figure 10). There may be a slight overall trend toward a smooth termination in larger specimens.

Ulrich and Resser (1930) used the shape of axial termination in the designation of several species. They suggested, for example, that *D. orbiculatus* had a "semi-elliptical bulblike termination rather than the slender obconical one seen in *D. hotchkissi*" (Ulrich and Resser, 1930:30). This analysis shows that there is no justification for using this character in specific designations.

POST-AXIAL RIDGE.—The axis appears to extend into a low and poorly-defined post-axial ridge in a small number of specimens (Labandeira and Hughes, 1994, pl. 1: fig. 14). Uncompressed material shows that even where this ridge is not developed, the dorsal surface arches upward slightly posterior of the axis (Hughes, 1993, pl. 6: fig. 6).

Ulrich and Resser (1930) suggested that *D. norwalkensis* (only found in the laminated sand subfacies) was characterized by the possession of a post-axial ridge. The prominence of this ridge was over-emphasised in the retouched photographs (e.g., Ulrich and Resser, 1930, pl. 21: fig. 16) and it is not a species-specific character among *Dikelocephalus*.

POST-AXIAL EMARGINATION.—The development of a slight post-axial emargination is common in *Dikelocephalus* from all localities (Plate 4: Figures 2, 3, Plate 5: Figure 12, Plate 11: Figures 3, 5). It probably represents an upward arch of the dorsal surface posterior of the axis, rather than a marked inflection of the margin (Plate 11: Figures 8, 9). A similar emargination has been recognized in *Cermatops discoidalis* (Salter) (Hughes and Rushton, 1990), where its prominence may depend on the orientation of the pygidium during preservation. Emargination appears to be present in many transversely macropygous pygidia. The post-axial emargination is present in large specimens of *Dikelocephalus* and the degree to which it is developed may be slightly size-influenced (Figure 11).

Ulrich and Resser (1930:39) noted that in some specimens the "posterior edge ... is gently sinuate" and considered this feature to be diagnostic of *Dikelocephalus raaschi*. Twenhofel (1945, pl. 88: fig. 3), found an emarginate specimen that differed from *D. raaschi* in other characters. In assigning this specimen to *D. oweni*, he commented that the validity of many of Ulrich and Resser's (1930) species was doubtful. The results above indicate that emargination is a variable character and is indicative of intraspecific variation.

NUMBER OF PLEURAL AND INTERPLEURAL FURROWS.—The combined number of pleural and interpleural furrows on the pygidium of *Dikelocephalus* varies between 7 and 10; most specimens show either 8 or 9 furrows. In some specimens the number of furrows on each side of the sagittal axis is asymmetrical. The score for these pygidia was calculated as the average between the two sides (as in Sheldon, 1987). The number of furrows is not obviously size or locality-related (Figure 12). There is no suggestion that the development of incipient axial rings beyond the fourth ring is related to an increased number of pleural and interpleural furrows. Hence, there is no clear relationship between the number of pleural furrows and the axial furrows of the pygidium.

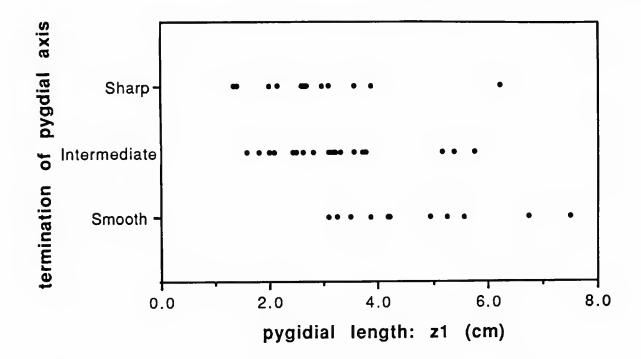Ulrich and Resser (1930) suggested that 9 to 10 ribs are

FIGURE 10.—Plot showing relationship between the shape of the axial termination and the length of the pygidium in *Dikelocephalus* from three localities in the St. Lawrence Formation; n = 47. Localities are LaGrange Mountain (RWa), North Freedom Bed 2 (NF2), and North Freedom Bed 8 (NF8).
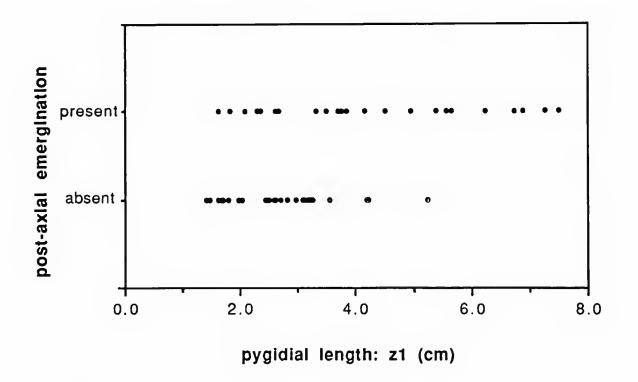

FIGURE 11.—Plot showing occurrence of a post-axial emargination in relationship to the length of the pygidium in *Dikelocephalus* from four localities in the St. Lawrence Formation; n = 62. Localities are LaGrange Mountain (RWa), Arcadia Bed 18 (A Aa), North Freedom Bed 2 (NF2), and North Freedom Bed 8 (NF8).

present in *Dikelocephalus* but did not use this variation in designating species.

DIVISION OF THE PLEURAE.—Variability in pleural division is a striking feature within *Dikelocephalus*. Unequal division reflects an enlarged propleural band. Pygidia from four localities within the heterolithic facies have been assigned to one of three character states: equal (e.g., Plate 3: Figure 12); subequal (e.g., Plate 3: Figures 15, 16); or unequal division of pleurae (e.g., Plate 3: Figure 14) (Figure 13A). Analysis

indicates that, within these localities, the wide variation in the division of the pleurae is not size-related. Subequal division is the most common condition in specimens from all localities. Slight variation may occur between localities (Figure 13B,C) but the pattern of pleural division is highly plastic. Hence the erection of species solely on this basis pleural division is unwarranted.

Dikelocephalus from the Tunnel City Group often show unequally divided pleurae with an enlarged and inflated
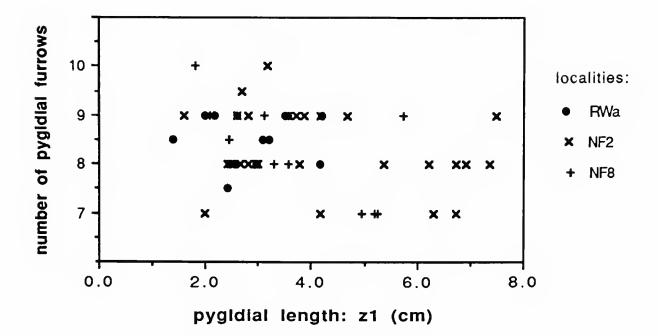
FIGURE 12.—Plot showing relationship between number of pygidial furrows and length of the pygidium in *Dikelocephalus* from three localities in the St. Lawrence Formation; n = 52. Localities are LaGrange Mountain (RWa), North Freedom Bed 2 (NF2), and North Freedom Bed 8 (NF8). Pygidial furrow number is the total number of pleural and interpleural furrows on the pygidium divided by 2.

propleural band (Plate 10: Figures 1–6, 13), but this condition is variable among specimens from the group (Labandeira and Hughes, 1994, pl. 1: figs. 12, 13). Similarly, within the laminated sand facies the pleural division may vary markedly (Ulrich and Resser, 1930; pl. 19: figs. 2, 4, 5, pl. 21: figs. 16–21). Material from the carbonate platform shows similar variability in pleural division (Plate 11: Figures 12, 13, 16). There is no reason to suggest that division of the pleurae is related to sedimentary facies, nor to particular localities.
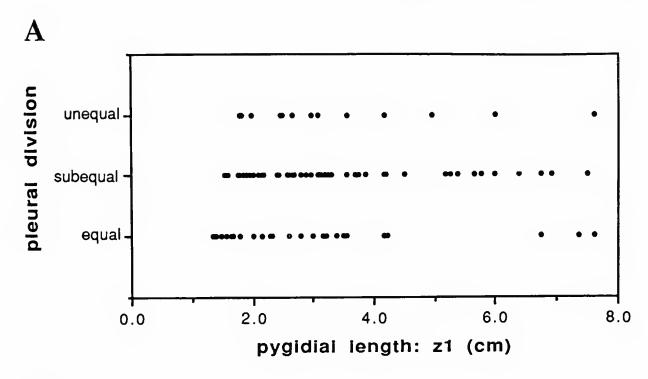
Raasch (1951) suggested that pleural division was size-related in *Dikelocephalus*. He commented that within the *Saukia sublonga* faunal unit (equivalent to the heterolithic facies of the *Saukia* fauna of Hughes, 1990) larger forms were characterized by unequal pleural division. The results of the present study do not support size control of pleural division. Even within localities there is no clear relationship between size and pleural division.
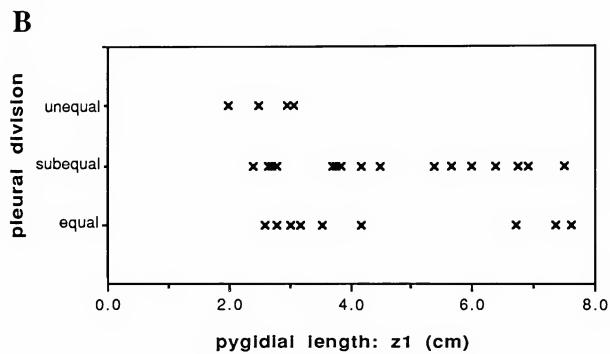
Winchell (1874:188) noted that the pleurae of *D. minnesotensis* were nearly equally divided "in their outer extension." Ulrich and Resser (1930) made frequent use of the variable pleural division in their species designations (Table 1). Forms such as *D. oweni*, *D. raaschi*, and *D. inaequalis* were supposedly characterized by unequal division. Labandeira (1983) measured the angle of divergence of the first three pleural furrows in Ulrich and Resser's type suite of specimens pooled from over 50 localities. His results indicated that the angle of divergence of all three furrows was variable, but a dsitinction of two or more morphs was not apparent (Labandeira and Hughes, 1994, fig. 4). Westrop (1986) referred specimens in a collection from Alberta to *D. oweni* and illustrated a tiny pygidium showing subequal pleural division (Plate 11: Figure 12; Westrop, 1986, pl. 3: fig. 4). He
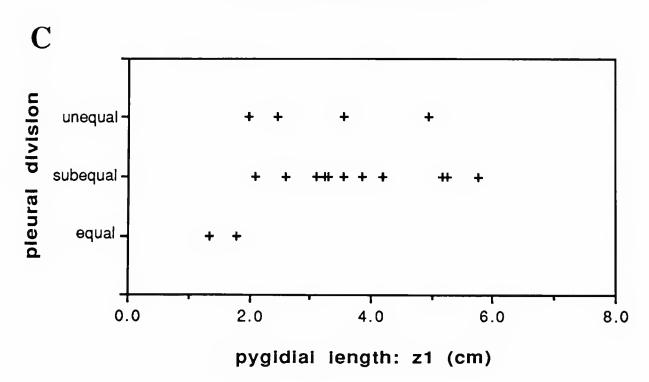
commented that a larger specimen (Plate 11: Figure 13) shows unequal division and short posterolateral spines, which were supposedly characteristic of this species. Westrop (1986:28) suggested that "subequally divided" pleurae were diagnostic of the genus. The present study suggests that pleural division is highly variable and that no single character state can be used to diagnose species of *Dikelocephalus*.

Where division is unequal in *Dikelocephalus*, it is the propleurae that are expanded relative to the opisthopleurae. This contrasts with the condition in the rest of the superfamily Dikelocephalacea (in the sense of Ludvigsen and Westrop, 1983a). In these taxa the opisthopleurae are swollen where division is unequal (e.g., *Briscoia septentrionalis* Kobayashi and "*Briscoia*" *elegans* (Kobayashi) Palmer, 1968, pl. 15: figs. 3, 4, 6, 7), although Ludvigsen and Westrop mistakenly suggested that propleurae of *Prosaukia hartii* (Walcott) expanded during ontogeny (Ludvigsen and Westrop, 1983a, text-fig. 6). Their plates (Ludvigsen and Westrop, 1983a, pl.10: figs. 5, 6, pl. 11: fig. 12, pl. 12: figs. 2, 3) show that there was expansion in the opisthopleurae throughout ontogeny.

LENGTH OF THE PLEURAE.—In their description and illustration of *D. marginatus*, Ulrich and Resser (1930) suggested that the first two pairs of pleural and interpleural furrows extended as far as, and converged with, the base of the posterolateral spine. Their retouched illustrations over-emphasised both the extent and the degree of convergence of these furrows. Possible convergence of the furrows is present in a few specimens (Plate 10: Figures 1–6, Plate 11: Figures 12, 16) but is not sufficiently widespread for this relationship to have been convincingly demonstrated. If furrows do converge at the base of the spine, this suggests that the spine is associated with at least two pygidial segments and is not homologous with marginal spines

FIGURE 13.—Plots showing relationship between division of the pleurae and pygidial length in *Dikelocephalus* from the St. Lawrence Formation; n = 91. A, Specimens are from four populations including LaGrange Mountain (RWa), Arcadia Bed 18 (A Aa), North Freedom Bed 2 (NF2), and North Freedom Bed 8 (NF8). B, Specimens from North Freedom Bed 2 only. C, Specimens from North Freedom Bed 8 only.

in *Parabriscoia* (Kobayashi, 1935), *Elkia* (Walcott, 1924a), and *Briscoia septentrionalis* (Palmer, 1968), which are direct extensions of individual opisthopleurae. The spines of the small pygidium from Alberta (Plate 11: Figure 12) do not appear to be related to the first pygidial segment. If this specimen is a late meraspid, which is likely given its small size, the anteriormost pygidial segment may be homologous with the last thoracic segment in adult holaspid *Dikelocephalus*.

MARGINAL RIM.—A large specimen from Galesville, Wisconsin (Twenhofel, 1945, pl. 88: fig. 3), has a narrow tubular rim developed on the margin of the doublure (Plate 11: Figures 3–5). This structure does not extend along the posterolateral spine. The rim has not been recorded in any other specimen, even of comparable size. As this pygidium is typical of *Dikelocephalus minnesotensis* in all other respects, the unique occurrence of this minor structure provides insufficient grounds for specific differentiation.

The pygidial border of *D. marginatus* was described as "rimmed" by Ulrich and Resser (1930:50). The nature of this rim was not discussed and re-examination of the syntypes does not suggest a rim on the pygidial margin.

ORNAMENTATION.—Pustulation on the pygidial axis is size-dependent and varies in a similar way to glabellar pustulation. Pustules are common in smaller specimens (Plate 3: Figures 14, 15, Plate 5: Figure 6, Plate 8: Figures 1, 2, 5, 6) and are not found in specimens with pygidial lengths (z1)

greater than about 5 cm. The pattern of pygidial ornamentation is similar to that on the glabella and suggests ontogenetic control of pustulation throughout the entire axis.

The ornament of other areas of the pygidium is variable. A small fragmented pygidium from the laminated sand subfacies near Mauston, Wisconsin, shows pustules on both the propleurae and opisthopleurae (Hughes, 1993, pl. 6: fig. 4). A medium-sized pygidium, from Hokah, Minnesota, shows tiny pustules developed only at the posterior margins of the pleurae (Hughes, 1993, pl. 6: fig. 3). As surface ornament is variable within collections, the unusual condition of these two specimens is not considered to be of taxonomic importance. The dorsal surface of most specimens is covered with inosculating terraces (more regular transverse ridges are present on the anterior facet of the first pleurae), which become crescentic or granular at the posterior of the terminal piece and on the pleural platform (Plate 5: Figures 6–12, Plate 8: Figures 2–8). There appears to be a gradational transformation from terraces into pustules towards the axis.

The terracing on the ventral surface of *Dikelocephalus* is much more regular than that on the dorsal surface. The distances between four or five terraces in the middle section of the doublure were combined to produce an average terrace spacing value. The analysis included specimens from both heterolithic and laminated sand facies. Correlation between terrace spacing and pygidial length is positive and strong (r = 0.974). Reduced major axis yields a regression coefficient of 1.059, strongly suggesting isometric increase in terrace spacing through growth, even though the sample size is small (n = 18). Hence, terrace spacing increases in direct proportion to pygidial length (Figure 14), and there is no evidence of allometry in terrace spacing during growth. There is little apparent locality
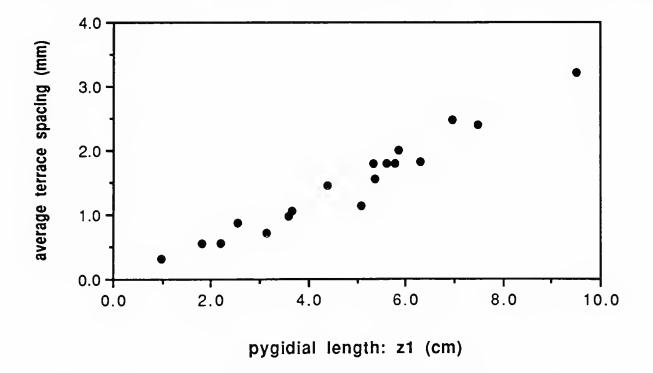

FIGURE 14.—Bivariate scatterplot showing relationship of average distance between terraced ridges on pygidial doublure (mean of five measurements) to pygidial length in *Dikelocephalus* from five localities in the northern Mississippi Valley; n = 18. Localities are Hell Hollow (HW), Lansing (LSb), Hickory Flat Road Quarry, Muscoda (MCa), North Freedom Bed 2 (NF2), and North Freedom Bed 8 (NF8). Hell Hollow and Lansing collections are from the Tunnel City Group.

TABLE 3.—Variation in nominal and ordinal characters in *Dikelocephalus*. Temporal variation implies a difference between specimens from the Tunnel City Group and the St. Lawrence Formation. Intercollection variation implies a clinal pattern of variation between localities. ? means too few data are available to establish this trend with confidence.

Character	Variation pattern			Comments
	Ontogenetic	Intrapopulational	Interpopulational	
CRANIDIA				
Anterior border		X	X	Associated variation in caeca and suture
Caeca		X	X	Assocated variation in anterior border
Eye position		X	X	Temporal variation; similar variation in specimens from outside the region
Eye ridge		X		
Glabellar anterior margin		X		
S3 furrows	?	X		
Intercalated furrows		X		
Confluence of S1 and S2 with axial furrow	?	X		
Median tubercle		X		
Possibly dimorphic				
Glabellar pustulation	X	X		Similar variation in specimens from outside the region
FREE CHEEKS				
Median suture		X		Possibly dimorphic
Marginal rim		X		
Genal spines		?		
Ornament		X		
HYPOSTOMES				
Median body	?	X		
Maculae	X	X		
THORAX				
Thoracic segment number		?		
Ornament		X		
PYGIDIUM				
Number of axial furrows		X		
Termination of axis	?	X		
Post-axial ridge		X		
Post-axial emargination	?	X		
Pygidial rib number		X		
Pleural division		X	X	Possible temporal variation
Ventral rim		X		
Dorsal ornament	X	X		
Ventral terracing		X		

or substrate influence on this character, as specimens from sandy facies of the Tunnel City Group fall within the same trend as specimens from the heterolithic facies (Figure 14).

DISCUSSION

Analysis of twenty-seven nominal and ordinal characters reveals considerable variability within northern Mississippi Valley *Dikelocephalus* (Table 3; see also Hughes, 1991, fig. 2). Seventeen of these characters were used by Ulrich and Resser (1930) in their species designations (Table 1), five of them were discussed by Labandeira (1983). This analyses shows that these characters provide no grounds for the recognition of more than a single morphospecies. The lack of discontinuous

variation within *Dikelocephalus* suggests that all specimens are part of a single morphospecies. This argument is strengthened by that fact that variations in nominal characters are almost all present within collections from single beds.

Several nominal and ordinal characters in *Dikelocephalus* show evidence of ontogenetic control (Table 2). Pustulation on the axis and maculae development on the hypostome become less prominent as overall size increases. Size-dependent variation in these characters is interesting because it generally is thought that trilobite morphology varies little during the holaspid stage (Shaw, 1956; Whittington, 1957, 1959; Saul, 1967; Pabian and Fagerstrom, 1968, 1972; Hu, 1971; Eldredge, 1972).

All the characters of *Dikelocephalus* discussed above show

variation within bedding plane collections (Hughes, 1991, fig. 2). Most show as much variation within, as they do between, collections. The few characters that do show locality-based differences also show significant intracollection variation. This suggests that intercollection differences are simply exaggerated intracollection variations. Within collections all major characters seem to show continuous variation. Even the two putative presence/absence characters (median tubercle and median suture) show gradational development and do not provide strong support for the presence of discrete morphs. There is limited evidence for temporal morphological changes in *Dikelocephalus*. The position of the eye appears constant within the St. Lawrence Formation, but varies both within and between collections in the Tunnel City Group. It is the only nominal and ordinal character that differs between the Tunnel City Group and St. Lawrence Formation collections. All *Dikelocephalus* from outside the northern Mississippi Valley lie within the range of variation present in the region. They also show some of the same intracollection variation. The variation of a few characters on the frontal area may be linked, but the vast majority of characters vary independently.

The marked intraspecific variation in nominal and ordinal characters in *Dikelocephalus* has implications for studies of other trilobites. For example, surface ornament has long been used as a taxonomically significant character in trilobites. It has been suggested that ornament is a "primary species characteristic" of Upper Cambrian trilobites (Palmer, 1960:53), and the presence of pustulation has been used to define many trilobite species (e.g., Ulrich and Resser, 1933; Chatterton and Perry, 1983; Eldredge, 1972, 1973). Analysis of *Dikelocephalus* shows that pustulation may show marked variation during the holaspid ontogeny of a single species, which falsifies the suggestion that ornament variation is necessarily species-specific (see also Stubblefield, 1926; Rasetti, 1948:9; Bright, 1959; Ludvigsen and Westrop, 1983a; Fortey and Owens, 1991). Although phenotypic variation in the pustules has been recorded (e.g., *Phacops*: Eldredge, 1972, 1973; *Dalmanites myops* (König): Ramsköld, 1985; Whittington and Evitt, 1953:31), little attention has been paid to the possibility of ontogenetic control of pustulation development. The recognition of ontogenetic regulation of pustule development within the holaspid stage of *Dikelocephalus* was dependent on detailed analysis of a large number of specimens. Pustulation may only be used to define species in cases where the ontogeny of pustules is well known.

This investigation of *D. minnesotensis* shows that many other characters previously considered "species-specific" actually represent intraspecific variation. Marked intraspecific variation in nominal and ordinal characters has also been documented in the holaspids of a variety of trilobite clades, including eodiscids (Jell, 1975, 1990); redlichides (Bergström and Levi-Setti, 1978); corynexochides (Rasetti, 1948; Robison, 1967); ptychoparioids (Bright, 1959); asaphides (Fortey and Shergold, 1984; Sheldon, 1987); encrinurids (Best, 1961;

Chatterton and Campbell, 1980; Strusz, 1980:23; trinucleids (Bertrand and Lespérance, 1971; Lespérance and Bertrand, 1976; Sheldon, 1987; Shaw, 1991); pterygometopids (Shaw, 1974:40); and phacopids (Eldredge, 1972). In the light of these results it seems likely that trilobite taxonomy is commonly too finely split and that the systematics of many taxa may be in need of substantial revision. This suggestion is not new (see Rasetti, 1948), but requires reiteration because new species continue to be errected on the basis of small numbers of specimens, with insufficient consideration of intraspecific variation.

Bivariate Analysis

INTRODUCTION

Nominal and ordinal characters present strong evidence for the wide range of morphological variation in *Dikelocephalus*, but are of limited value in determining the likely controls on this variation. Quantitative comparisons of sclerite dimensions, which are discussed in this section, allow a more detailed examination of controlling mechanisms responsible for morphological variation. Bivariate analysis, by facilitating detailed examination of sclerite growth relationships, enables resolution of more subtle morphological variation.

APPROACH.—Bivariate analyses examine the relationships between pairs of variables through growth. Labandeira's (1983) bivariate work on Ulrich and Resser's (1930) type suite demonstrated that each pair of variables shows a single trend line through holaspid growth. Labandeira and Hughes (1994) examined the variation of 24 variables using a combined univariate, bivariate, and multivariate approach to study Ulrich and Resser's (1930) species, and were unable to discriminate more than one morphospecies. Labandeira (1983) did not discuss growth in detail but concluded that all the growth relationships are isometric and show little dispersion about the general trend. The work reported in this section aims to document and account for patterns of variability within *Dikelocephalus*. Characters used in bivariate analysis were selected from the suite of 24 characters previously studied by Labandeira and Hughes (1994) (Table 3; Figure 3). The overall pattern of morphological variability in *Dikelocephalus* was assessed by multivariate techniques.

METHODS.—Labandeira and Hughes' (1994) study of the pooled type-suite of *Dikelocephalus* was not designed to reveal locality-related variation. To investigate such variation required extensive material from well-documented sites. Although large numbers of specimens were available many proved to be unsuitable for morphometric analysis of some characters.

The methods of measurement and character choice are discussed in the introduction. All reduced major axis (RMA) analyses in this section were computed using logarithms of the original measurements. A consequence of using logarithms is

over-emphasis of variation among smaller specimens. This explains the seemingly high values for the coefficients of variation in collections composed of small specimens. Standard abbreviations for sclerite dimensions were used (Table 3; Figure 3).

The morphological variation in each character is assessed with reference to a standard measure for size. The standard chosen for the cranidium is the occipital-glabellar length (b1), and for the pygidium it is the intra-articulating pygidial length (z1). These dimensions were selected because axial features tend be relatively invariant in trilobites (Palmer, 1957).

RESULTS

Cranidium

GLABELLAR WIDTH.—The overall shape of the glabella was assessed by examining the relationship between the occipital lobe width and the occipital-glabellar length. A pooled sample from five localities (including Tunnel City Group specimens) yields a very strong correlation between these two dimensions (r = 0.993) and there is little variation in glabellar shape in the sample (Figure 15). Specimens from outside the northern Mississippi Valley fall within this range of variation. The growth of the glabella is positively allometric at the 95% significance level. There are no significant differences in the glabellar shape among collections.

The growth relationships were examined using reduced major axis (RMA) and correlation coefficients. The reduced major axis of the pooled sample (log values of all specimens from all collections) shows a growth ratio of 1.076, suggesting allometric growth ($p<0.05$). Comparison of the glabellar width/length ratio (k/b1) to glabellar length (b1) (Figure 16) also shows a significant positive correlation (r = 0.470, $p<0.01$). This suggests that slight ontogenetic increase in the relative width of the glabella may occur within the collection. This correlation could reflect the fact that collections characterized by narrower glabellae have lower mean sizes, but there is also significant correlation between the ratio and size within individual collections. The collection with the largest size range (NF8) shows a significant correlation between the ratio and overall size (r = 0.322, $p<0.05$). Within Stillwater (SWb), Tunnel City Group (TCG), and Arcadia (A Aa) collections there is an apparent tendency for the ratio to increase through growth, although these relationships are not statistically significant, perhaps due to the small sample sizes. Glabellar length/width relationships are the ones most likely to be distorted by compression and deformation, because the dimensions are orthogonal and the glabella is vaulted (Hughes and Jell, 1992). The correlation coefficient for glabellar length/width in Dikelocephalus is the highest of all pairwise correlation coefficients in the cranidium (Table 18). Hence the effects of compression appear to be slight compared to original biological variation within Dikelocephalus, provided that

TABLE 4.—Reduced major axes for occipital lobe width/occipital-glabellar length in Dikelocephalus from four St. Lawrence Formation localities and a pooled sample from the Tunnel City Group. (a represents the slope equation; b represents the intercept value on the y axis (in this case the y axis is the occipital lobe width [k]). NF2 = North Freedom Bed 2; NF8 = North Freedom Bed 8; A Aa = Arcadia Bed 18; SWb = Stillwater; TCG = pooled sample from Tunnel City Group.)

Locality	a	b
All	1.076	−0.120
NF2	1.020	−0.082
NF8	1.053	−0.116
A Aa	1.068	−0.112
SWb	1.061	−0.120
TCG	1.138	−0.132

TABLE 5.—Coefficients of relative dispersion about reduced major axis of occipital lobe width/occipital-glabellar length.

Locality	Coefficient of relative dispersion
NF2	4.34
NF8	8.11
A Aa	14.12
SWb	14.45
TCG	59.02

obviously deformed specimens are excluded from the data set prior to analysis. The growth allometry in glabellar shape is nearly masked by size-independent phenotypic variation within samples, as the within-collection correlation coefficients between glabellar width/length and glabellar length are low and the degree of scatter about the trend is high (Figure 16).

Reduced major axes for the five collections all show similar slope values (b) (Table 4) suggesting that the growth relationship governing glabellar shape was very similar in all localities (Figures 15, 16). No collection-based differences are apparent among the St. Lawrence Formation collections (Plates 1–4, 6, 7, 9). The complete overlap at the 95% confidence level suggests that there is continuous variation throughout the sample, even though there are statistically significant differences between the Tunnel City Group and North Freedom Bed 2 collections. This statistical difference may be attributed to the different mean sizes of these collections.

The coefficient of dispersion was calculated for each locality to assess whether localities showed different degrees of intracollection variation (Table 5). There are differences in the coefficient between the collections, but the level of intracollection variation is relatively constant within St. Lawrence Formation localities. The greater variation within the Tunnel City Group sample is probably due to the pooling of specimens from several localities.

The morphology of the glabella is often considered conservative at low taxonomic levels in trilobites (Stubblefield, 1936; McNamara, 1986) and hence variation in glabellar form has been used extensively in the taxonomy of the Dikelo-
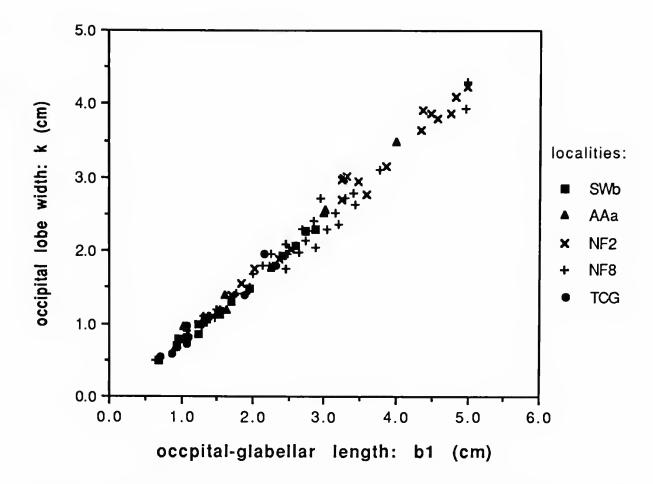
FIGURE 15.—Bivariate scatterplot showing relationship between occipital-glabellar length and occipital lobe width in *Dikelocephalus* from five localities in the northern Mississippi Valley; n = 105. Localities are Stillwater (SWb), Arcadia Bed 18 (A Aa), North Freedom Bed 2 (NF2), North Freedom Bed 8 (NF8), and a pooled sample from the Tunnel City Group (TCG).
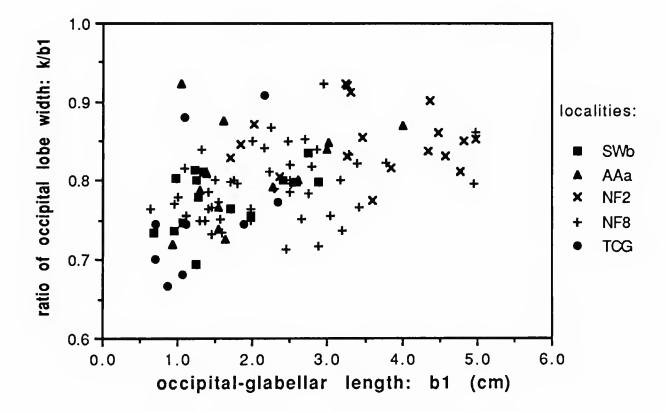
FIGURE 16.—Bivariate scatterplot showing ratio of occipital lobe width divided by occipital-glabellar length plotted against occipital-glabellar length. Data set as in Figure 15.

cephalidae (Ulrich and Resser, 1930; Lochman, 1959). The limited variation in glabellar shape in *Dikelocephalus* suggests that all specimens are closely related. Ulrich and Resser (1930) made use of the relative width/length ratio in their taxonomy of *Dikelocephalus* (Table 1). Large species, such as *D. orbiculatus*, had small glabellar length/width ratios (Ulrich and Resser, 1930:29), whereas small species, such as *D. edwardsi*, had larger length/width ratios (Ulrich and Resser, 1930:49). This analysis shows that these variations are not species-specific and may reflect slight allometric growth of the glabella. Labandeira (1983) assessed the relationship between occipital-glabellar length (b1) and width (k) within Ulrich and Resser's type suite and found an almost identical correlation (r = 0.994) to that found in this study.

FRONTAL AREA LENGTH.—Growth of the frontal area is slightly positively allometric. There is great size-independent variation in frontal area length both within and between localities but there is no justification for the recognition of more than one morphotype. *Dikelocephalus* from outside the northern Mississippi Valley region have frontal area lengths within the range shown by specimens in the region.

The relationship between frontal area length (f1) and occipital-glabellar length (b1) was assessed using specimens from six localities within the St. Lawrence Formation and a pooled sample from the Tunnel City Group (Table 6). The relatively low correlation coefficient for the total sample reflects the high degree of variability in frontal area length (r = 0.934) (Figures 17–19). The growth of the frontal area is positively allometric at the 95% confidence level, although the relative increase in frontal area length was all but swamped by phenotypic variation and is not particularly variable in *Dikelocephalus*. The reduced major axis of the pooled sample shows a specific growth ratio of 1.116, suggesting positive allometric growth ($p<0.05$). However, the ratio of frontal area length to occipital-glabellar length (f1/b1) is not correlated with occipital-glabellar length (b1) (r = 0.032), which suggests that this allometry is slight. Analyses of individual collections demonstrate that only the pooled Tunnel City Group collections show both significant positive allometry of the frontal area (Figure 20; Plate 9: Figures 1–5, 7–11, 16). The allometry in the Tunnel City Group collection is suprising because the specimens come from six localities. It could be an artifact of pooling the specimens or it may be a difference that exists between *Dikelocephalus* from the Tunnel City Group and St. Lawrence Formation. Removal of the Tunnel City Group collection from the data set does not significantly alter the correlation coefficient of the total sample.

There is great variation in the length of the frontal area relative to occipital-glabellar length both within and between collections (Figures 17–19; Plate 2: Figures 1–3, 6, 7, Plate 3: Figures 1–6, Plate 4: Figures 1–9, Plate 6: Figures 1–14). Although there is a significant difference at the 95% confidence level between the collections with the greatest difference in slope equations (Tunnel City Group and North Freedom Bed

TABLE 6.—Reduced major axes for frontal area length/occipital-glabellar length in *Dikelocephalus* from six St. Lawrence Formation localities and a pooled sample from the Tunnel City Group. (a represents the slope equation; b represents the intercept value on the y axis (in this case the y axis is the frontal area length [f1]). NF2 = North Freedom Bed 2; NF8 = North Freedom Bed 8; A Aa = Arcadia Bed 18; SWa = Fairy Glen, Stillwater; SWb = Stillwater; LRc = Button Bluff; TCG = pooled sample from Tunnel City Group.)

Locality	a	b
All	1.116	−0.487
NF2	0.997	−0.443
NF8	1.024	−0.403
A Aa	1.020	−0.439
SWa	1.082	−0.543
SWb	1.037	−0.542
LRc	1.140	−0.617
TCG	1.284	−0.412

TABLE 7.—Coefficients of relative dispersion about reduced major axis of frontal area length/occipital-glabellar length.

Locality	Coefficient of relative dispersion
NF2	25.17
NF8	21.68
A Aa	20.20
SWa	30.66
SWb	28.84
LRc	22.99
TCG	20.26

2), there is overlap among all seven collections. This suggests that the pattern of variation of the frontal area is clinal. Variation in the ratio of frontal area length to occipital-glabellar length (f1/b1) is continuous throughout the sample and is not correlated with overall size; there are no apparent subgroups within collections. No ratio value is exclusive to a particular collection and frontal area length cannot be used to discriminate between taxonomic groups. It is, however, possible to recognize end-members within the total range of variation and this may suggest a clinal pattern of variation in frontal area length.

Reduced major axes show that some collections differ significantly in respect of frontal area length (Table 6). There are some differences in levels of intracollection variation (Table 7; Figures 17–20). Some localities show relatively constant frontal area lengths throughout the collection (i.e., Arcadia Bed 18; Figure 17), whereas others show great variation (i.e., North Freedom Bed 2 and Stillwater). Within collections, the range of the ratio of frontal area length to occipital-glabellar length (f1/b1) is similar in both small and large cranidial size classes (Figures 14–17), which suggests that variance is not size-related.

In spite of the fact that there are significant differences between collections (Arcadia [A Aa] and Button Bluff [LRc] collections show almost no overlap; Figure 19a), it is impossible to identify the provenance of specimens with
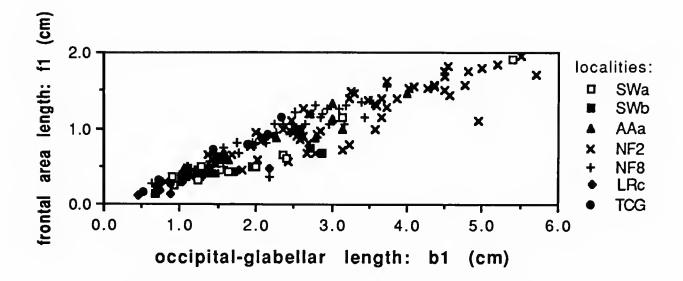
FIGURE 17.—Bivariate scatterplot showing relationship between occipital-glabellar length and frontal area length in *Dikelocephalus* from seven localities in the northern Mississippi Valley; n = 171. Localities are Fairy Glen, Stillwater (SWa), Stillwater (SWb), Arcadia Bed 18 (A Aa), North Freedom Bed 2 (NF2), North Freedom Bed 8 (NF8), Button Bluff (LRc), and a pooled sample from the Tunnel City Group (TCG).
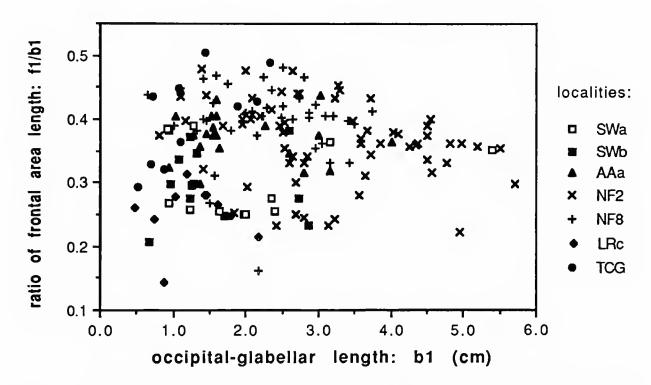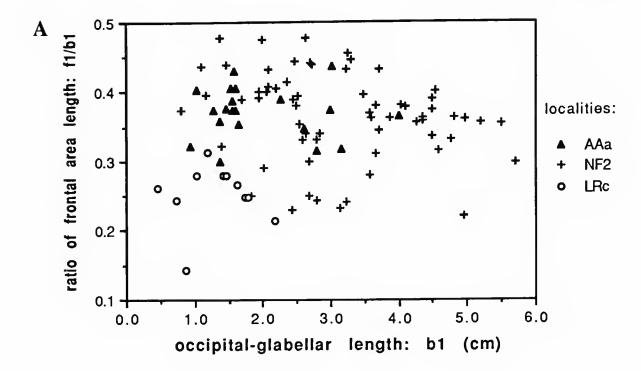
FIGURE 18.—Bivariate scatterplot showing ratio of frontal area length divided by occipital-glabellar length plotted against occipital-glabellar length. Data set as in Figure 17.

confidence on the basis of frontal area length. Variation in the frontal area lengths is considerable both within and between collections. There are no grounds for recognizing particular morphs or subspecies within the sample. *Dikelocephalus* cranidia from Nevada, Montana, and Alberta show a range of frontal area/occipital-glabellar length ratios from 0.227 to 0.389. This range is within that shown by northern Mississippi Valley specimens (0.143 to 0.503) and there is no reason to think that the specimens from outside the region represent different taxa.

The name *Dikelocephalus,* literally "shovel head," indicates the prominence of the frontal area, the relative length of which has been used as an important taxonomic character. The "width

of the brim" was one of the most important criteria used by Ulrich and Resser (1930:8) in the recognition of species. They established two groups of species within *Dikelocephalus* largely on the basis of frontal area morphology. The *oweni* group was characterized by broad frontal areas, and the *gracilis* group was characterized by short frontal areas. The analysis above shows that there is no justification for the use of this character in specific differentiation.

In some Early Paleozoic trilobites the border may shorten during the holaspid phase (Hu, 1971), but the ontogenies of many primitive libristomate species show a progressive increase in the length of the frontal area relative to overall size through the meraspid and into the holaspid periods (e.g.,
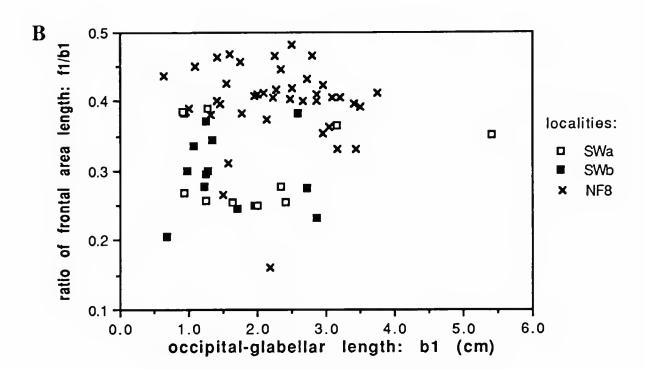
FIGURE 19.—Plots showing relationship between ratio of frontal area length dividied by occipital-glabellar length against occipital-glabellar length in *Dikelocephalus* from the St. Lawrence Formation. A, Specimens from Arcadia Bed 18 (A Aa), North Freedom Bed 2 (NF2), and Button Bluff (LRc); n = 96. B, Specimens from Fairy Glen, Stillwater (SWa), Stillwater (SWb), and North Freedom Bed 8 (NF8); n = 65.

Pterocephalia concava Palmer: Palmer, 1965; *Taenicephalus shumardi* (Hall): Hu, 1981; *Idahioa wisconsinensis* (Owen) and *Orgymaspis (Parabolinoides) contracta* (Frederickson): Westrop, 1986; *Hundwarella personata* Reed: Hughes and Jell, 1992). *Dikelocephalus* likewise shows slight positive allometry in the length of the frontal area.

Relative lengths of the frontal area have often been considered to be of taxonomic importance in other primitive libristomate trilobites (e.g., Palmer, 1962:34; Hu, 1981) although wide variation in frontal area length is known within Late Cambrian (Longacre, 1970, fig. 8) and Early Ordovician

(Fortey, 1974, fig. 3) species. The width of the frontal area in *Dikelocephalus* partly reflects whether the facial suture was marginal or retracted (see above). Cranidia with relatively long frontal areas are those that possess an inflated anterior border (Plate 3: Figures 2–4, Plate 6: figures 1–14).

FRONTAL AREA WIDTH.—The width (tr.) of the frontal area (j2) shows marked variation in *Dikelocephalus* (e.g., Plate 2: Figures 1–7, Plate 3: Figures 1–6, Plate 4: Figures 4–8, Plate 6: Figures 1–14). The length of the glabella (b1) and frontal area width (j2) show a high positive correlation (0.980), and the variance of frontal area width both within and between most
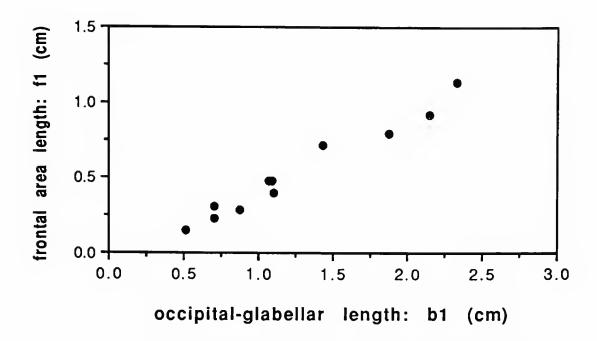
FIGURE 20.—Bivariate scatterplot showing relationship between occipital-glabellar length and frontal area length in a pooled sample from the Tunnel City Group (TCG); n = 11.

localities is relatively low. Growth of frontal area width is positively allometric at the 95% confidence level. Patterns of locality-based variation (Figures 18, 19) in frontal area width mimic those shown by frontal area length.

A correlation of the ratio of the frontal area width to occipital-glabellar length (j2/b1) with occipital-glabellar length (b1) shows a significant but small positive correlation (0.259, $p<0.01$), confirming the general pattern of positive allometry of frontal area width. This correlation may be due to the different size ranges of the specimens in collections. Those collections that have specimens showing relatively narrow frontal areas tend to have smaller mean sizes than those having wider brims (Figures 21, 22), leading to the increased proportion of narrow brimmed forms at smaller sizes. Within individual collections there is no significant correlation between size (as expressed by the occipital-glabellar length) and relative width of the frontal area. Hence, if growth of frontal area width is allometric it is only slightly so, because large sample sizes are needed to detect it.

The slope values (a) are variable among localities but there are no significant differences between collections at the 95% confidence level. The range of variation within the samples is continuous and although specimens in some collections tend to have wider frontal areas than others, these differences do not provide adequate grounds for taxonomic subdivision of *Dikelocephalus*. Unlike the variation in frontal area length, there is overlap of the confidence limits of the reduced major axes of all collections (Table 8) and thus there is no strong suggestion of clinal variation in frontal area width.

Analysis of the ratio of frontal area width/occipital-glabellar length compared to occipital-glabellar length from the seven collections shows similar patterns to those shown in frontal area lengths. This is because there is a strong positive correlation between frontal area length and width (r = 0.955),

which is higher than the correlation between occipital-glabellar length and frontal area length (r = 0.934). Hence where the frontal areas are broad they also tend to be wide. However, frontal area width is most highly correlated with occipital-glabellar length (r = 0.980). This suggests that the length of the frontal area is more variable than its width and explains why although some collections show significant differences in frontal area length, they do not show significant differences in frontal area width. It appears that frontal area morphology does not vary as a strictly integrated unit.

Intracollection variability was assessed using the coefficient of relative dispersion about the reduced major axis (Table 9). Tunnel City Group (TCG) and Button Bluff (LRc) collections showed substantially higher variation than did collections from other localities. In the case of the Tunnel City Group this may be due to the pooling of specimens from several localities, but this cannot explain the high levels of variation within Button Bluff. There are slight differences in the level of intralocality variability within the other collections. Ranking of collections

TABLE 8.—Reduced major axes for frontal area width/occipital-glabellar length in *Dikelocephalus* from five St. Lawrence Formation localities and a pooled sample from the Tunnel City Group. (a represents the slope equation; b represents the intercept value on the y axis (in this case the y axis is the frontal width length [j2]). NF2 = North Freedom Bed 2; NF8 = North Freedom Bed 8; A Aa = Arcadia Bed 18; SWb = Stillwater; LRc = Button Bluff; TCG = pooled sample from Tunnel City Group.)

Locality	a	b
All	1.078	0.117
NF2	1.009	0.152
NF8	1.036	0.154
A Aa	0.995	0.114
SWb	1.063	0.100
LRc	0.961	0.094
TCG	1.111	0.102
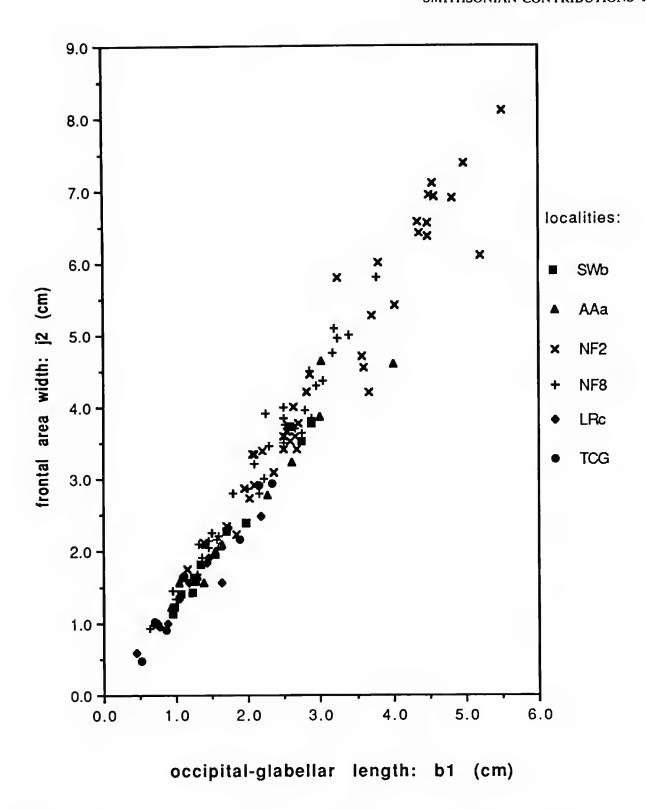
FIGURE 21.—Bivariate scatterplot showing relationship between occipital-glabellar length and frontal area width in a pooled sample of *Dikelocephalus* from six localities in the northern Mississippi Valley; n = 125. Localities are Stillwater (SWb), Arcadia Bed 18 (A Aa), North Freedom Bed 2 (NF2), North Freedom Bed 8 (NF8), Button Bluff (LRc), and a pooled sample from the Tunnel City Group (TCG).

TABLE 9.—Coefficients of relative dispersion about reduced major axis of frontal area width/occipital-glabellar length.

Locality	Coefficient of relative dispersion
NF2	7.12
NF8	7.06
A Aa	11.95
SWb	8.98
LRc	40.49
TCG	60.82

in terms of the levels of intracollection variability reveals substantial differences in the order obtained for frontal area length and width. This suggests that a portion of the variation in frontal area length and width is independent.

Ulrich and Resser (1930) frequently used the width of the frontal area in their species designations. They viewed the frontal area as an integrated unit and characterized species on both its length and width (Ulrich and Resser, 1930:8). Raasch (1951) suggested that his revised taxa *D. minnesotensis* and *D. oweni* differed in the breadth of the frontal area. Labandeira
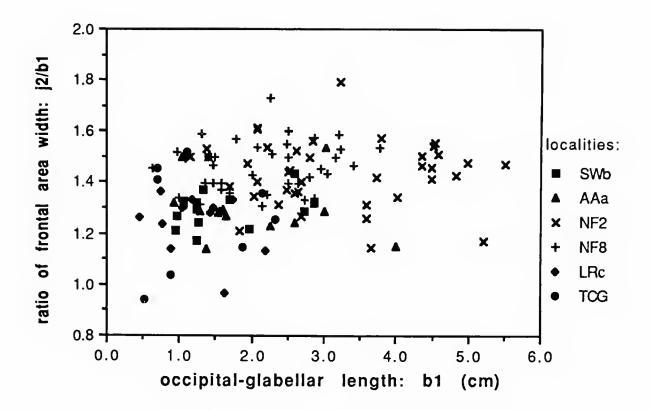
FIGURE 22.—Bivariate scatterplot showing ratio of frontal area width divided by occipital-glabellar length plotted against occipital-glabellar length. Data set as in Figure 21.
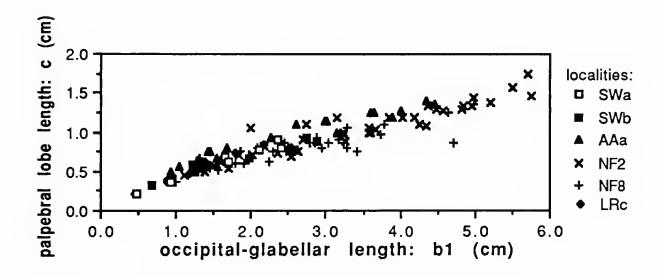

FIGURE 23.—Bivariate scatterplot showing relationship between occipital-glabellar length and palpebral lobe length in a pooled sample of *Dikelocephalus* from six localities in the St. Lawrence Formation; n = 131. Localities are Fairy Glen, Stillwater (SWa), Stillwater (SWb), Arcadia Bed 18 (A Aa), North Freedom Bed 2 (NF2), North Freedom Bed 8 (NF8), and Button Bluff (LRc).

(1983) did not discuss frontal area width. The present analysis shows that there is no justification for species designations based on frontal area morphology.

PALPEBRAL LOBE LENGTH.—The relative length of the palpebral lobe decreases during ontogeny, remaining negatively allometric throughout holaspid growth. The rate at which the eye length/occipital-glabellar length ratio decreases progressively diminishes and the allometry is negligible at larger sizes. This trend is consistent within six collections from St. Lawrence Formation localities. *Dikelocephalus* from outside

the northern Mississippi Valley area follow the same trend and lie within the range of variability present among northern Mississippi Valley specimens.

The pooled sample from all six collections shows a curvilinear trend between palpebral lobe length (c) and occipital-glabellar length (b1) (Figure 23; Hughes, 1991, fig. 3). The ratio of the two variables changes as overall size increases. The trend line flattens through growth (Figure 23), meaning that the allometry is negative. Hence, the relative length of the palpebral lobe compared to that of the glabella

decreased through ontogeny. Reduced major axis analysis shows significant negative allometry (Table 10; also see Plate 2: Figures 1–3, 6–8, Plate 3: Figures 1–6, Plate 4: Figures 4–9, Plate 6: Figures 2–13, Plate 9: Figures 1, 3, 9, 11, 15). A logarithmic regression function describes the relationship between palpebral lobe length (c) and occipital-glabellar length (b1) (Hughes, 1991, fig. 3). This suggests that a constant growth control operated throughout the holaspid period. Correlations can only be calculated when the data are adjusted to account for the logarithmic nature of the relationship of palpebral lobe length (c) and occipital-glabellar length (b1). The correlation coefficient (r) for the pooled data set is 0.945.

The ratio of palpebral lobe length to occipital-glabellar length (c/b1) is size-dependent (Figure 24). In specimens with glabellae longer than about 4 cm, the ratio stabilized to a value of about 0.3, and remained constant thereafter. Growth of the eye in cranidia with glabellae larger than 4 cm (sag.) was effectively isometric. The influence of locality on the relationship between palpebral lobe length and occipital-glabellar length was investigated using reduced major axes. Axes were calculated for the entire collection and from each individual locality to assess the significance of any locality-based variation (Table 10).

The low values of the slope equation (Table 10) indicate negative allometry of the palpebral lobe, which is significant at the 95% confidence level in all collections. The two most dissimilar values are those of Arcadia (A Aa) and the Fairy Glen locality at Stillwater (SWa); these collections show a significant difference in growth allometry (at $p < 0.05$). However, the differences between all pairs of most similar localities are not significant and hence the variation within the whole sample is

continuous and appears clinal. There is no reason to suspect that the intercollection variation in the growth of the palpebral lobe represents more than intraspecific variation. In the bivariate plot (Figure 23) specimens from Arcadia (A Aa) are concentrated along the top of the trend line (Hughes, 1991, fig. 3) although they overlap considerably with specimens from other localities. In the initial instars of holaspid ontogeny, *Dikelocephalus* specimens from Arcadia had relatively large palpebral lobes compared to specimens from all other localities (see Plate 3: Figures 1–6).

The coefficients of relative dispersion suggest that specimens from most localities had a similar degree of variation about the general growth trend of the palpebral lobe (Table 11; Figures 23, 24). The collection from the Fairy Glen locality (SWa) shows the relatively little intracollection variation, which is surprising because this collection includes specimens showing unusually large variability in frontal area morphology. Similarly, collections from Arcadia (A Aa) and North Freedom Bed 8 (NF8) show marked intraspecific variation, but show little variation in frontal area length relative to specimens in other collections.

Although the palpebral lobe has been mentioned in previous studies of *Dikelocephalus* its allometric growth has not been noted by previous workers. The size of the palpebral lobe was often used by Ulrich and Resser (1930) to characterize their species. For example *D. gracilis* was considered to have "relatively much larger eyes" than *D. minnesotensis* (Ulrich and Resser, 1930:43). The syntype specimens used to define *D. gracilis* were much smaller than those assigned to *D. minnesotensis*.


FIGURE 24.—Bivariate scatterplot showing ratio of palpebral lobe length divided by occipital-glabellar length plotted against occipital-glabell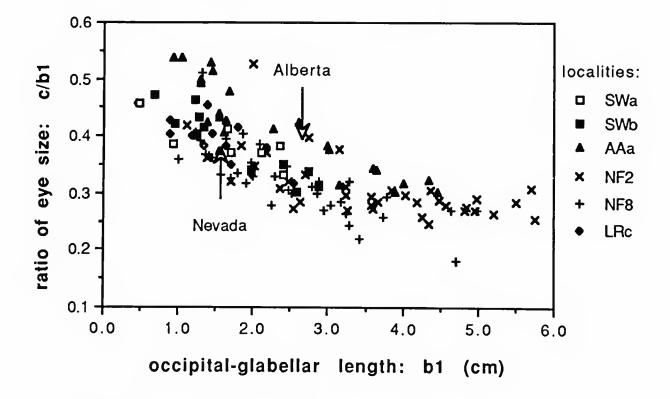ar length. Data set as in Figure 23. Arrows point to positions of *Dikelocephalus minnesotensis* Owen specimens from outside the northern Mississippi Valley.

TABLE 10.—Reduced major axes for palpebral lobe length/occipital-glabellar length in *Dikelocephalus* from six localities. (a represents the slope equation; b represents the intercept value on the y axis (in this case the y axis is the palpebral lobe length [c]). NF2 = North Freedom Bed 2; NF8 = North Freedom Bed 8; A Aa = Arcadia Bed 18; SWa = Fairy Glen, Stillwater; SWb = Stillwater; LRc = Button Bluff; TCG = pooled sample from Tunnel City Group.)

Locality	a	b
All	0.736	−0.368
NF2	0.773	−0.396
NF8	0.688	−0.385
A Aa	0.678	−0.289
LRc	0.855	−0.383
SWa	0.871	−0.391
SWb	0.709	−0.361

TABLE 11.—Coefficients of relative dispersion about reduced major axes for palpebral lobe length/occipital-glabellar length.

Locality	Coefficient of relative dispersion
NF2	15.58
NF8	22.99
A Aa	19.95
LRc	16.76
SWa	13.11
SWb	14.97

Pygidium

PYGIDIAL WIDTH.—The shape of the pygidium is virtually invariant throughout holaspid growth and between collections. There appears to be a slight positive allometry within some St. Lawrence Formation collections as the post-axial border shortens, but the results are ambiguous.

The intra-articulating pygidial length (z1) and the maximum pygidial width (w) show a rectilinear relationship with a low degree of scatter (Figure 25). The correlation coefficient, calculated for a pooled sample from seven localities, is high ($r = 0.991$) (Tunnel City Group specimens were included in this correlation) and the growth relationship does not differ significantly from isometry at the 95% confidence level. Plots of the ratio of pygidial width to length (w/z1) against overall size (z1) show striking differences between localities (Figure 26). Specimens from the Tunnel City Group generally have higher width/length ratios than do most specimens from the St. Lawrence Formation (Figure 26; Plate 9: Figures 17–20, Plate 10: Figures 1–13), but this may be due partly to the small mean size of the Tunnel City Group specimens.

Among the Tunnel City Group sample there is an apparent ontogenetic increase in the length of the postaxial border relative to the pygidial width, but the reduced major axis analysis shows that this relationship is not significant at the 95% confidence level. Correlation of the ratio of pygidial width/length with overall size, however, suggests significant negative allometry ($r = 0.533$, $p<0.05$). Interpretation of the

meaning of this trend is difficult because the sample is pooled from seven different localities none of which yields the full range of holaspid sizes. The trend could be an artifact caused by pooling different collections or caused by an allometric growth control.

Pygidia from six St. Lawrence Formation localities show the same correlation coefficient ($r = 0.991$) as that of the entire sample (Tunnel City Group and St. Lawrence Formation specimens) but do not suggest negative allometry in pygidial width (Table 12). Some collections even show slight positive allometry (Table 12). For example, specimens from Stillwater (SWb) show ontogenetic decrease in the length of the pygidium (Figure 26; Plate 2: Figures 13–16). Correlation of the width/length ratio with overall size for this collection confirms this relationship ($r = 0.749$, $p<0.01$).

The reduced major axes show some variation in intercept and slope values between localities, but this is largely due to the wide size range over which pygidial length and width vary (Table 12).

Within the whole sample there is continuous overlap of the 95% confidence levels of the reduced major axes, but there are significant differences among specimens from North Freedom Bed 2 and those from North Freedom Bed 8, Arcadia Bed 18, and Stillwater (SWb). There seems to be no difference between the North Freedom Bed 2 and Arcadia specimens (Figure 26). More small specimens from these localities are needed to resolve whether the differences in reduced major axes are really valid, but even if this proves to be the case, the pattern of variation within the whole sample seems to be clinal.

Some differences in the degree of intracollection variation in pygidial morphology occur but there are no striking differences between localities (Table 13). Pygidial shape was not one of the main criteria upon which Ulrich and Resser (1930) based their taxonomy of *Dikelocephalus*. However, they referred to slight differences in pygidium length/width ratios that were consistent among species. *Dikelocephalus ovatus* was distinguished from *D. gracilis* by its "very slightly greater length" (Ulrich and Resser, 1930:45) and *D. orbiculatus* differed from *D. hotchkissi* in "its relatively greater length" of the pygidium (Ulrich and Resser, 1930:45). The revised *D. minnesotensis* was considered to differ from *D. oweni* in its "narrower and more elliptical" pygidium (Raasch, 1951:142). Labandeira (1983) plotted length/width relationships of 124 of Ulrich and Resser's specimens and found no evidence for any more than a single trend line within the whole sample (Labandeira and Hughes, 1994, fig. 9).

PYGIDIAL AXIAL LENGTH.—Axial length is variable within *Dikelocephalus*. Growth of the axis is almost isometric with respect to pygidial length. The axis is generally longer in Tunnel City Group specimens than in St. Lawrence Formation specimens, but there is considerable overlap among all collections.

Although the axis is a discrete morphological region in *Dikelocephalus*, the point of its termination is often difficult to
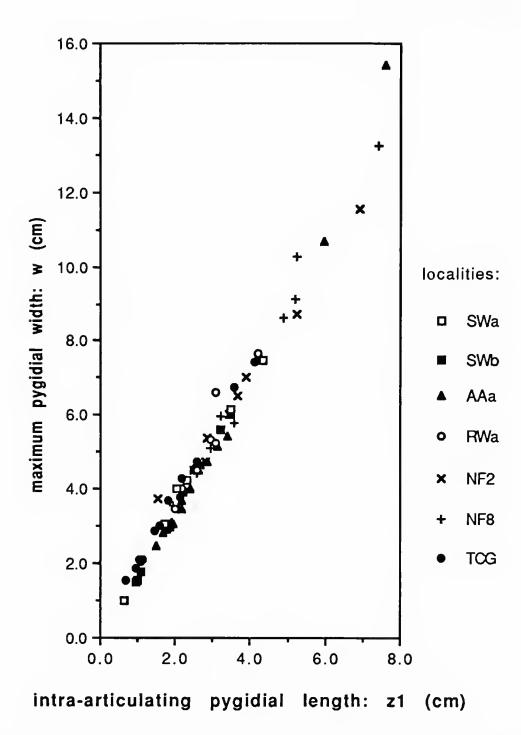
FIGURE 25.—Bivariate scatterplot showing relationship between pygidial width and intra-articulating pygidial in a pooled sample of *Dikelocephalus* from seven localities in the northern Mississippi Valley; n = 75. Localities are Fairy Glen, Stillwater (SWa), Stillwater (SWb), Arcadia Bed 18 (A Aa), LaGrange Mountain (RWa), North Freedom Bed 2 (NF2), North Freedom Bed 8 (NF8), Button Bluff (LRc), and a pooled sample from the Tunnel City Group (TCG).

define. Variation in the shape of the terminal piece has been documented above. In this analysis the point of termination was taken as the base of the slope along the sagittal axis from axis to border. In specimens with a post-axial ridge the termination was defined as the break of slope from axis to ridge. Because this slope is frequently smooth (compare Plate 8: Figures 4, 9, Plate 9: Figure 19) some of the variation in axial lengths may reflect difficulty in identifying the termination.

There is a strong correlation between axis length (y1) and pygidium length (z1) (r = 0.983) (Figure 27), and the reduced major axis indicates isometric growth in the pooled sample at the 95% confidence level. Most of the scatter about the growth trend line reflects the difference between Tunnel City Group and St. Lawrence Formation collections (Figures 27, 28).

Collections from Stillwater (SWb) and LaGrange Mountain (RWa) show significant positive allometry of the axis length (at $p<0.05$; Table 14). In LaGrange Mountain specimens this allometry may be an artifact of small sample size, as allometry is not obvious in plots of the ratio of axial length/pygidial length against pygidial length. Stillwater (SWb) specimens show significant positive allometry in axis length with respect to posterior border length. This is supported by a significant correlation ($r = 0.643, p<0.05$) of the axial/pygidial length ratio value with overall size. Most of the small pygidia that were studied came from the Stillwater (SWb) collection; they may reveal a slight positive allometry that is typical of all St. Lawrence *Dikelocephalus* but that was undetectable in larger holaspids.
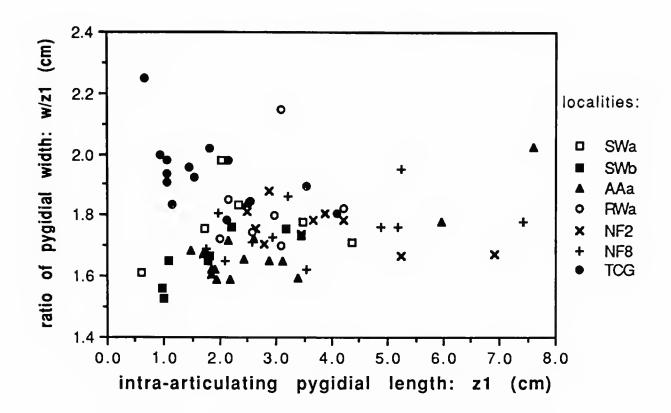
FIGURE 26.—Bivariate scatterplot showing ratio of pygidial width divided by intra-articulating pygidial length plotted against intra-articulating pygidial length. Data set as in Figure 25.

TABLE 12.—Reduced major axes for pygidial width/pygidial length in *Dikelocephalus* from seven localities. (a represents the slope equation; b represents the intercept value on the y axis (in this case the y axis is the pygidial width [w]). NF2 = North Freedom Bed 2; NF8 = North Freedom Bed 8; AAa = Arcadia Bed 18; RWa = LaGrange Mountain, Redwing; SWa = Fairy Glen, Stillwater; SWb = Stillwater; TCG = pooled sample from Tunnel City Group.)

Locality	a	b
All	0.994	0.203
NF2	0.933	0.283
NF8	1.050	0.218
AAa	1.099	0.188
RWa	1.027	0.237
SWa	1.044	0.236
SWb	1.099	0.201
TCG	0.936	0.300

TABLE 13.—Coefficients of relative dispersion about reduced major axes for pygidial length/pygidial width.

Locality	Coefficient of relative dispersion
NF2	2.00
NF8	3.08
AAa	3.69
RWa	2.52
SWa	5.85
SWb	3.33
TCG	5.51

Specimens from LaGrange Mountain (RWa) and Stillwater (SWb) show significant positive allometry and are significantly different from those of the North Freedom Bed 2, but there is continuous overlap among all the collections. The reduced major axis of the Tunnel City Group specimens lies within the range shown by St. Lawrence Formation specimens. Plots showing the ratio of axial to pygidial length confirm that there is little allometry in the growth of the pygidium (Figure 28), and indicate continuous overlap in the ranges of variation throughout all collections. Variation in the length of the axis does not provide grounds for the taxonomic subdivision of *Dikelocephalus*. The Tunnel City Group shows the greatest level of intracollection variation (Table 15), probably because the sample is pooled from different localities.

Ulrich and Resser (1930) did not use the relative length of the axis as an important taxonomic character within *Dikelocephalus*, although they frequently commented on its shape. Lochman (1959) suggested that the axis extended along three-fifths of the pygidium. *Dikelocephalus freebergensis* Feniak, from the Tunnel City Group, was described as having a axial length "three-fourths of that of the pygidium" (Bell, Feniak, and Kurtz, 1952). A plot of axial length was included in Labandeira's (1983) thesis and showed a single trend line. However, Labandeira (1983) did not include Tunnel City Group specimens in his bivariate analysis.

POSTEROLATERAL SPINE.—The relative length of the posterolateral spines decreased throughout holaspid ontogeny in all collections of *Dikelocephalus*. There is marked locality-based variation in spine morphology.

A decrease in the relative length of the spine through ontogeny can be detected in all the collections (Plate 2: Figures
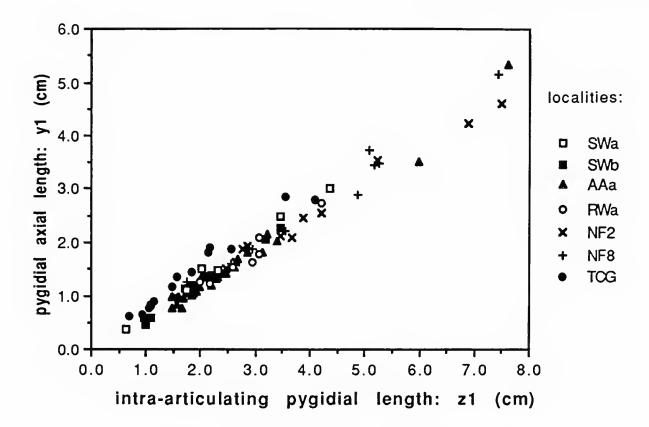
FIGURE 27.—Bivariate scatterplot showing relationship between pygidial axial length and intra-articulating pygidial length in a pooled sample of *Dikelocephalus* from seven localities in the northern Mississippi Valley; n = 92. Localities are Fairy Glen, Stillwater (SWa), Stillwater (SWb), Arcadia Bed 18 (A Aa), LaGrange Mountain (RWa), North Freedom Bed 2 (NF2), North Freedom Bed 8 (NF8), Button Bluff (LRc), and a pooled sample from the Tunnel City Group (TCG).
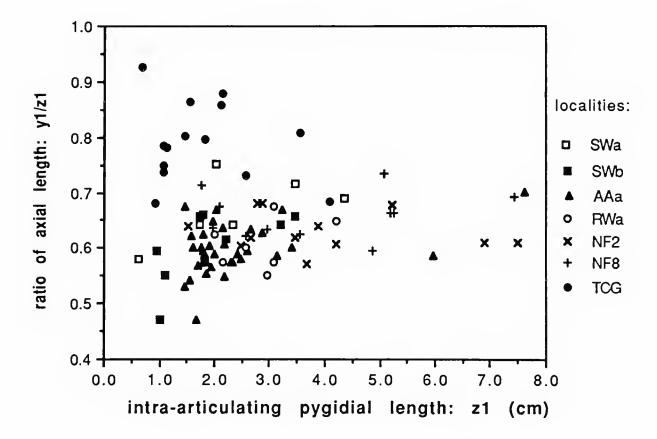

FIGURE 28.—Bivariate scatterplot showing ratio of pygidial axial length divided by intra-articulating pygidial length plotted against intra-articulating pygidial length. Data set as in Figure 27.

TABLE 14.—Reduced major axes for axial length/pygidial length in *Dikelocephalus* from seven localities. (a represents the slope equation; b represents the intercept value on the y axis (in this case the y axis is the pygidial width [w]). NF2 = North Freedom Bed 2; NF8 = North Freedom Bed 8; A Aa = Arcadia Bed 18; RWa = LaGrange Mountain, Redwing; SWa = Fairy Glen, Stillwater; SWb = Stillwater; TCG = pooled sample from Tunnel City Group.)

Locality	a	b
All	1.023	−0.202
NF2	0.982	−0.192
NF8	1.019	−0.192
A Aa	1.095	−0.257
RWa	1.121	−0.272
SWa	1.103	−0.207
SWb	1.176	−0.264
TCG	0.988	−0.101

TABLE 15.—Coefficients of relative dispersion about reduced major axes for axial length/pygidial length.

Locality	Coefficient of relative dispersion
NF2	4.99
NF8	5.72
A Aa	11.68
RWa	8.21
SWa	11.00
SWb	19.19
TCG	25.46

13–16, Plate 3: Figures 12–16, Plate 4: Figures 1–3, Plate 5: Figures 6–12, Plate 8: Figures 1–13, Plate 10: Figures 1–13). The length of the spine was assessed by measuring the dimension z5 (the intra-articulating pygidial spine length; Shaw, 1956:206). This dimension was chosen as it is difficult to define exactly where the spine joins the pygidial border.

The relationship between spine length and pygidial length is curvilinear (Figure 29) and negatively allometric within all collections. The correlation coefficient between spine length and pygidium size, calculated using logarithms, is high (r = 0.972) and the allometry is significant at well above the 95% confidence level. The ratio of spine/pygidium length (z5/z1) diminishes as overall size increases (Figure 30), and at larger sizes the allometry is undetectable. Reduced major axes indicate that the allometry in spine length is significant within all localities (Table 16).

There is a striking difference in the relative spine length among localities (Figures 29, 30), but reduced major axes show that there is a continuous and clinal pattern of variation in growth trends among the collections. The z5/z1 ratio is size-dependant (Figure 30). Pygidia from Arcadia (A Aa) show unusually long spines, but the slope value is lower than at most other localities. This means that the rate at which the spine length decreases is faster at Arcadia than at all other localities. Hence the growth parameters controlling spine growth were slightly different in the Arcadia collection than in other

collections. The slopes derived from Arcadia specimens and from those of both North Freedom collections differ significantly at the 95% confidence level. However, the slope of the Arcadia collection is influenced by the presence of two large specimens which show short spines. An increased number of large specimens is necessary to test the significance of the reduced major axis of the Arcadia collection.

The coefficients of relative dispersion for the Tunnel City Group and Arcadia collections are much higher than among other collections (Table 17). Variation within the Tunnel City Group is probably the result of pooling samples from several localities. Within the St. Lawrence Formation the Arcadia collection shows the greatest level of intracollection variation, which may be reflected in the unusually long spines among some specimens from this locality.

The posterolateral spines have been recognized as an important feature in *Dikelocephalus* since the original description of *D. minnesotensis* (Owen, 1852). Ulrich and Resser (1930:18) included the spines in their list of taxonomically important variables and made frequent use of them in species descriptions. Raasch (1951) noted that small specimens were characterized by longer spines than larger specimens and attributed this to ontogenetic variation. Labandeira (1983) considered spine variation to be intraspecific but did not suggest possible controls.

A small pygidium (likely meraspid) of *Dikelocephalus* from

TABLE 16.—Reduced major axes for intra-articulating pygidial length and the posterolateral spine length in *Dikelocephalus* from five St. Lawrence Formation localities and a pooled sample from the Tunnel City Group. (a represents the slope equation; b represents the intercept value on the y axis (in this case the y axis is the posterolateral spine length [z5]). NF2 = North Freedom Bed 2; NF8 = North Freedom Bed 8; A Aa = Arcadia Bed 18; RWa = LaGrange Mountain, Redwing; SWa = Fairy Glen, Stillwater; TCG = pooled sample from Tunnel City Group.)

Locality	a	b
All	0.819	0.104
NF2	0.888	0.433
NF8	0.875	0.052
A Aa	0.711	0.203
RWa	0.851	0.111
SWa	0.827	0.071
TCG	0.829	0.086

TABLE 17.—Coefficients of relative dispersion about reduced major axes for pygidial spine length/pygidial length (z5/z1).

Locality	Coefficient of relative dispersion
NF2	4.71
NF8	2.90
A Aa	12.53
RWa	5.02
SWa	4.86
TCG	11.69
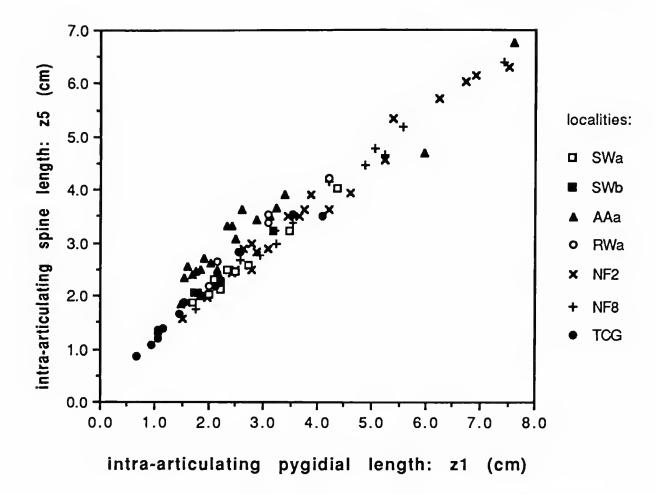
FIGURE 29.—Bivariate scatterplot showing relationship between intra-articulating pygidial spine length and intra-articulating pygidial length in a sample of *Dikelocephalus* from seven localities in the northern Mississippi Valley; n = 92. Localities are Fairy Glen, Stillwater (SWa), Stillwater (SWb), Arcadia Bed 18 (A Aa), LaGrange Mountain (RWa), North Freedom Bed 2 (NF2), North Freedom Bed 8 (NF8), Button Bluff (LRc), and a pooled sample from the Tunnel City Group (TCG).
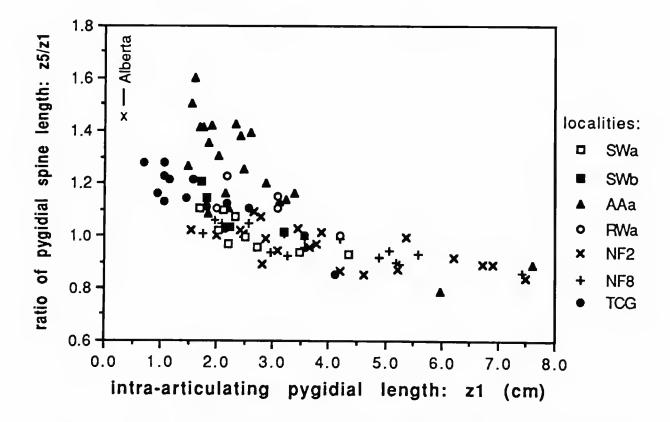

FIGURE 30.—Bivariate scatterplot showing ratio of intra-articulating pygidial spine length divided by intra-articulating pygidial length plotted against intra-articulating pygidial length. Data set as in Figure 29.

TABLE 18.—Growth controls and intrapopulational variation in crandia and pygidia of *Dikelocephalus*. Cranidial measurements are correlated with occipital-glabellar length (b1). Pygidial measurements are correlated with intra-articulating pygidial length (z1). Localities are Fairy Glen, Stillwater (SWa), Stillwater (SWb), Arcadia Bed 18 (A Aa), North Freedom Bed 2 (NF2), North Freedom Bed 8 (NF8), and a pooled sample from the Tunnel City Group (TCG).

Statistic	Glabellar width (k)	Frontal area length (f1)	Frontal area width (j2)	Palpebral lobe length (c)	Pygidial width (w)	Axial length (y1)	Spine length (z5)
Correlation coefficient (r)	0.993	0.934	0.980	0.945	0.991	0.983	0.972
RMA coefficient (a)	1.076	1.116	1.078	0.736	0.994	1.023	0.819
Overall growth relationship	Allometric	Allometric	Allometric	Allometric	Isometric	Isometric	Allometric
Significant differences in growth rates	NF2 : TCG	NF2 : TCG	None	A Aa : SWa	NF2 : A Aa, SWa, NF8	NF2 : SWb	A Aa : NF2, NF8

Alberta preserves a single extremely long spine (Plate 11: Figure 12; Westrop, 1986). The pygidium fits exactly on the general growth curve for specimens from the St. Lawrence Formation and suggests that *Dikelocephalus* specimens outside the northern Mississippi Valley were subject to growth controls similar to those that operated within the region.

DISCUSSION

The results indicate a variety of growth controls in *Dikelocephalus* and high levels of intraspecific variation both within and among collections. A portion of the variation of most characters is independent. The growth of many characters is allometric.

GROWTH CONTROLS.—Bivariate analysis provides a means of resolving important growth controls that nominal and ordinal character analyses are unable to detect. Size-dependent variation was clearly demonstrated in two nominal and ordinal characters, and suggested in several others. Bivariate methods have detected allometries in many other characters. The lengths of the palpebral lobe and the posterolateral spines show strong allometry in holaspids, but most other characters show some size-related variation (Table 18). The recognition of allometry in most of the bivariate characters is important because it helps to reconcile the observation of great morphological variation within *Dikelocephalus* (Ulrich and Resser, 1930) with the recognition of a single morphospecies (Labandeira, 1983). Ulrich and Resser (1930) did not recognize any size-related variation within *Dikelocephalus* and interpreted these variations as species-specific. Labandeira's (1983) bivariate plots showed that specimens are usually tightly clustered about a single trend line, suggesting a single morphospecies (Labandeira and Hughes, 1994). These contrasting interpretations can now be accounted for by allometric variation (Hughes, 1991).

Allometric variation in sclerite dimensions during the holaspid phase has been recognized in many trilobite taxa (e.g., olenellides: Cowie and McNamara, 1978; emuellids: Pocock, 1970; redlichiides: Westergård, 1936; Pillola, 1991; agnostids: Jell and Robison, 1978; eodiscids: Jell, 1975; corynexochides: Robison, 1967; ptychopariids: Bright, 1959; Schwimmer,

1989; olenids: Kaufmann, 1933; asaphides: Jaanusson, 1953; Shergold, 1972; Hughes, 1979; Ludvigsen, 1979; Fortey, 1980; Fortey and Owens, 1991; proetides: Pabian and Fagerstrom, 1968, 1972; Tremblay and Westrop, 1991; cheirurids: Whittington, 1957; and dalmanitids: Shergold, 1966; Ramsköld, 1985). Inspite of widespread occurrence of allometry, most reviews of trilobite growth suggest that growth in holaspid trilobites is isometric (Shaw, 1956; Whittington, 1957, 1959; Pabian and Fagerstrom, 1968, 1972; Eldredge, 1972). This misapprehension arose because isometric growth relationships are common in holaspid growth, and because holaspid allometry is usually limited compared to the allometries of earlier growth phases. Furthermore, rectinlinear growth relationships among sclerite dimensions have commonly been interpreted to indicate isometric growth without being tested statistically (e.g., Temple, 1957; Selwood, 1966; Saul, 1967; Strusz, 1980; Chatterton and Ludvigsen, 1976).

Allometric growth is accompanied by an overall increase in morphological variability within *Dikelocephalus* and other trilobites (an exception being *Ameura missouriensis* (Shumard) Pabian and Fagerstrom, 1972, fig. 12). This is because a small change in the initial growth conditions will have a more profound affect on groups showing significant allometry than on groups showing strict isometry (Imbrie, 1956; Bright, 1959; Hartnoll, 1982; McNamara, 1986). A consequence of this relationship is that trilobites with high levels of allometry will often appear more morphologically plastic than those with few allometries.

POPULATION-RELATED VARIATION.—Much of the morphological variability in *Dikelocephalus* is locality-related (Hughes, 1991). Some characters (Table 18), such as the length of the frontal area, show remarkable plasticity both within and between collections. Specimens from some localities are characterized by short frontal areas (Button Bluff), and others are characterized by long frontal areas (North Freedom Bed 8), specimens from other localities cover the complete range of frontal area length (Fairy Glen, Stillwater, North Freedom Bed 2). Patterns of variation between localities suggest intraspecific clinal variation, although it is not possible to demonstrate that variation in the length of the frontal area length is related to

TABLE 19.—Coefficients of relative dispersion about reduced major axis showing intercollection variation in cranidia and pygidia of *Dikelocephalus*. Cranidial measurements are computed against occipital-glabellar length (b1). Pygidial measurements are computed against intra-articulating pygidial length (z1). X indicates no data for this population. Data set as in Table 18.

Locality	Glabellar width (k)	Frontal area length (f1)	Frontal area width (j2)	Palpebral lobe length (c)	Pygidial width (w)	Axial length (y1)	Spine length (z5)
North Freedom Bed 2 (NF2)	4.34	25.17	7.12	15.58	2.00	4.99	4.71
North Freedom Bed 8 (NF8)	8.11	21.68	7.06	22.99	3.08	5.72	2.90
Button Bluff (LRc)	X	22.99	40.49	16.76	X	X	X
LaGrange Mountain, Redwing (RWa)	X	X	X	X	2.52	8.21	5.02
Arcadia Bed 18 (A Aa)	14.12	20.20	11.95	19.95	3.69	11.68	12.53
Fairy Glen, Stillwater (SWa)	X	30.66	X	13.11	5.85	11.00	4.86
Stillwater (SWb)	14.45	28.84	8.98	14.97	3.33	19.19	X
Tunnel City Group (TCG)	59.02	20.26	60.82	X	5.51	25.46	11.69

environmental conditions. Clinal variation in most characters (Table 18) contrasts with the analysis of nominal and ordinal characters, in which clinal variation was recognized only in a small proportion of the total variation. Recognition of clines in the bivariate analysis is likely to be the result of the increased accuracy of this technique because much of the clinal variation recognized statistically is not immediately obvious from qualitative examination of specimens. Different characters show different clinal patterns and no consistent pattern of clinal variation is apparent. The refined stratigraphy (Hughes, 1990) indicates that the St. Lawrence Formation prograded southwards through time. It is not possible to detect patterns of morphological variation that track this temporal shift.

Non-biological factors, such as compaction or time-averaging are unlikely to have had significant influence on the intra- and intercollection patterns of variation. Those features most likely to have been affected by compaction (such as glabellar shape) show the least variation within collections, suggesting that compaction accounts for an insignificant amount of variation within *Dikelocephalus*. The patterns of variation in *Dikelocephalus* are unlikely to be influenced by variations in the degree of time-averaging because the different collections apparently show approximately similar levels of variability, even though individual characters show independent patterns of variation. The mosaic patterns of character variation could result from time-averaging of temporal clines within collections, but such an explanation is contrary to most sedimentological evidence (Hughes, 1990) and would require an extraordinary pattern of deme isolation. Even if correct, it would not invalidate the recognition of marked intraspecific variation within *Dikelocephalus*. Hence it appears likely that intracollection variations caused by taphonomic processes are negligible and are minor compared to original biological variations within the sample, which putatively represent individuals living at approximately the same time.

INTRASPECIFIC HETEROCHRONY.—There are intercollection differences in several allometric controls. The possession of large eyes and long posterolateral spines is a feature of younger

Dikelocephalus. The presence of both extraordinarily large eyes and long spines in young holaspids from Arcadia suggests the retention in adulthood of some juvenile features. This may have been achieved by slight change in the controls of development. By late in the holaspid period Arcadia specimens are similar to those from other localities, and so this developmental difference is only expressed in younger individuals. To determine the exact nature of these developmental changes requires detailed knowledge of the initial differentiation of these characters during early ontogeny. This is not possible in *Dikelocephalus* because the pre-holaspid ontogeny is unknown. Shifts in developmental timing are often interpreted as being indicative of heterochronic evolution (e.g., McNamara, 1986). The slight shifts in developmental regulation of the palpebral lobe and posterolateral spines in *Dikelocephalus* do not result in significant differences between Arcadia specimens and other collections, and so they cannot be regarded as indicating different morphospecies, especially as large holaspids are indistinguishable. They imply a pattern of heterochronic variation within a species, as has been described in modern fiburalid echinoids (McNamara, 1990) and Ordovician bryozoans (Pachut, 1989). Whatever the precise nature of the heterochrony in *Dikelocephalus* (both paedomorphic and peramorphic processes could explain the observed pattern depending on whether the shift represents early onset of mineralization, or prolonged expression of juvenile features) the developmental shift was not global in effect. This is indicated by the loss of pustules from cranidia at Arcadia over the same size range (i.e., at the same developmental stage) as in other collections (Figure 7). Hence the pattern of developmental regulation is dissociated (in the sense of McKinney, 1984) and implies independent character variation during ontogeny.

TUNNEL CITY GROUP *Dikelocephalus*.—The Tunnel City Group shows greater intracollection variation than any of the collections from the St. Lawrence Formation (Table 19). This is almost certainly due to the pooling of specimens from many localities. There is considerable variability in the frontal area width and above average variability in all characters except the

length of the frontal area (Table 19). There are slight interlocality differences within Tunnel City Group specimens, but compared to St. Lawrence Formation specimens they all possess expanded propleurae and relatively short post-axial borders, (Plate 9: Figures 17–20, Plate 10: Figures 1–13). A temporal trend toward expanded post-axial borders may occur within the two units. There is also marked intracollection variation within the Tunnel City Group in some cranidial characters (Plate 9: Figures 1–16), but small sample sizes prevent full documentation of this variation. Although some specimens from the Tunnel City Group appear to be strikingly different from those in the St. Lawrence Formation bivariate analysis shows considerable overlap of Tunnel City Group *Dikelocephalus* with the St. Lawrence Formation specimens in all characters. There are no consistant grounds for the recognition of separate morphospecies within the two units.

CHARACTER INDEPENDENCE.—Correlation analysis shows that some characters are more variable than others (Table 18), but all characters show independent patterns of variation. This confirms the results of nominal character analysis. The amount of variation of each character can vary widely between collections (Table 19). The similar patterns of variation in frontal area length and width suggests covariance (Table 19). However, this is the only indication of interdependent character variation, apart from covariance due to overall size. Arcadia and North Freedom Bed 8 collections show relatively little variation in the frontal area morphology, but both show a greater level of flexibility in palpebral lobe growth compared to specimens from other collections. Arcadia and North Freedom Bed 8 specimens themselves differ in the degree of intracollection variability of the posterolateral spine. It is not possible to determine which collections are inherently more variable than others, because characters vary independently and the coefficients of relative dispersion are dependent on the size ranges of the characters analyzed. Within any collection variability in one character can be accompanied by stasis in another; the pattern of variation among characters is mosaic.

Bivariate studies of trilobite dimensions document considerable intraspecific variation in many taxa (e.g., Lower Cambrian emuellids: Pocock, 1970; *Crassifimbra walcotti* (Resser): Palmer, 1958; *Paradoxides davidis* Salter: Bergström and Levi-Setti, 1978; *Elrathia kingii* (Meek): Bright, 1959; Upper Cambrian ptychopariids: Longacre, 1970; *Triarthrus*: Cisne, Chandlee, Rabe, and Cohen, 1980; Cisne, Molenock, and Rabe, 1980; *Flexicalymene*: Cisne et al., 1982). Much of this variation occurs within collections, but in some cases geographic and temporal clines have been recognized. Other taxa, such as *Phacops* from the Devonian of New York State (Eldredge, 1972), show low degrees of intraspecific variation that is limited to a small number of characters, among which variation is tightly coordinated and is related to a geographic cline.

Multivariate Analysis

INTRODUCTION

Nominal, ordinal, and bivariate character analyses have demonstrated great morphological plasticity both within and between collections of *Dikelocephalus*. However, these techniques suffer from the disadvantage that only a single character or pair of characters is examined in each analysis. Multivariate analysis assesses the variations of several characters synoptically and is useful for examining the detailed structure of variation among specimens (see Labandeira and Hughes, 1994).

Bivariate analysis indicates that all *Dikelocephalus* should be assigned to a single morphospecies. However, it is possible that subtle but discrete patterns of covariance among sclerite dimensions, which would reveal the presence of more than one morphospecies, might not be detected by bivariate analysis. Each bivariate relationship was established using a slightly different set of specimens (due to incomplete preservation) and this might have obscured distinctions within collections. Hence a variety of multivariate analyses were performed to examine the distribution of specimens in "morphospace" (i.e., multivariate space defined by the morphological variables analyzed). The pattern of morphospace occupation allows assessment of (1) whether discrete subgroups are present in the *Dikelocephalus* data set and (2) the patterns of intracollection variation are present in *Dikelocephalus*. These analyses used only the best preserved specimens from the St. Lawrence Formation and the Tunnel City Group. Characters selected were those most likely to be useful in the documentation of patterns of intraspecific variation within *Dikelocephalus*, based on previous multivariate examination of a wide variety of characters and sclerites (Labandeira and Hughes, 1994). Results suggest that all St. Lawrence Formation *Dikelocephalus* are best considered a single morphospecies, *D. minnesotensis*. Some, if not all, specimens from the Tunnel City Group also belong to *D. minnesotensis*.

MULTIVARIATE METHODS.—The multivariate techniques used included principal component analysis (PCA) and nonmetric multidimensional scaling (MDS). The MDS procedure used principal coordinate axes as trial vectors for MDS iterations. Analyses were performed on a Macintosh Classic using the BIOΣTAT II Multivariate Toolbox (produced by Pimentel and Smith, 1986).

PRINCIPAL COMPONENT ANALYSIS.—R-mode principal component analysis (PCA) was used to assess morphological variation within a sample of specimens from five localities in the northern Mississippi Valley. Relationships among specimens were simplified by calculating the position of each individual as a point in multivariate space (or morphospace), the coordinates of which are defined by the variables analyzed. Because six characters were measured from each cranidium, the cranidial morphospace is six-dimensional; for pygidia the

morphospace is four dimensional. If the characters covary individuals will distribute along vectors within the morphospace. The tightness of clustering about these vectors is a measure of the covariance of the specimens (for details of PCA see Reyment et al., 1984).

The most obvious variation between specimens is in size. Specimens of different sizes will occupy different positions in morphospace, but as size is an important variable, it is likely that a size-related vector will be distinguished as the first principal component. This vector may also contain an element of shape variation, particularly if shape variation is strongly correlated with size. Other vectors will describe additional variations, and these may be independent of size. Principal component analysis identifies the coordinates of these vectors (known as principal component axes) and assesses how much of the total variance is accounted for by each. The way in which the variation is distributed among the principal components provides information on the interrelationships between the input variables. The more constrained the degree of variation within *Dikelocephalus*, the larger the proportion of the total variation accounted for by the few first principal components. Principal component analysis determines the number of components needed to describe all significant variations and assesses the contribution of each variable to each vector, providing a measure of the degree of covariance within the sample. Because principal components anlaysis explicitly documents the relationship between the input variables and the resultant ordination it is particularly useful for assessing patterns of character variation.

Principal components analyses were run separately on the cranidia and pygidia. All characters except angular measures of the cranidium, were linear measurements. Data were standardized by calculating z-scores of the original data (Pimentel, 1981) in order to remove the effects of unequal size ranges of the original variables. Principal components were then calculated.

Principal component analysis of *Dikelocephalus* reveals that the first principal component accounts for well over 80% of the total variance within the sample. In several analyses it accounts for more than 95% of the variance. The first principal component is mostly a reflection of differences in overall size, which cannot be considered of taxonomic significance in *Dikelocephalus* (Hughes, 1993). Other styles of morphological variation are concentrated in subsequent principal components, which account for a tiny proportion of the total variance. As such their significance is doubtful. In order to determine whether these principal components have "captured" useful information it is necessary to compare the the patterns of variation determined using principal component analysis with results obtained by other analyses of the same data set (Pimentel, 1981).

NONMETRIC MULTIDIMENSIONAL SCALING.—Principal component analysis effectively identifies styles of variation that affect all individuals within a data set. As a consequence the

TABLE 20.—Correlation matrix of cranidial characters of the multivariate sample of *Dikelocephalus* from the St. Lawrence Formation (n = 45). Underlining indicates statistical significance at the 99.9% confidence level.

	b1	f1	j2	< of div.	c	k
b1		0.949	0.976	0.271	0.932	0.991
f1	0.949		0.955	0.376	0.881	0.946
j2	0.976	0.955		0.371	0.889	0.975
< of div.	0.271	0.376	0.371		0.170	0.282
c	0.932	0.881	0.889	0.170		0.929
k	0.991	0.946	0.975	0.282	0.929	

ordination produced does not necessarily reflect the true pattern of differences between individuals. Multidimensional scaling, calculated on the basis of a matrix of proximities between individuals, produces ordinations in which the spatial distribution of individuals in morphospace closely approximate their actual similarities (Kruskal and Wish, 1977). The association coefficient used to calculate the proximites was Euclidean distance, and the configurations of individuals represent the morphological distances between individuals in the way that a map represents spatial distances between locations. As such, multidimensional scaling is very useful for identifying patterns of morphospace occupation (see Labandeira and Hughes, 1994, for a more detailed discussion of the application of multidimensional scaling to studies of *Dikelocephalus*). It does not make a priori assumptions of group membership and hence is not subject to the procedural difficulties presented by multiple discriminant analysis. The cranidial and pygidial data sets were standardized by calculating a matrix of z-scores prior to running MDS.

RESULTS

CRANIDIA.—Principal component anlaysis.

St. Lawrence Formation Specimens: A correlation matrix calculated of specimens included in the principal component analysis accords well with the bivariate study, as expected (see Tables 18 and 20).

As in bivariate analysis, the highest correlation values are between the two measurements of glabellar shape, b1 and k. This high correlation suggests that postmortem deformation due to taphonomic processes has been slight (see discussion in bivariate section above). The correlation coefficients of the angle of divergence with other variables are low. This result is to be expected because angular meaurements may be independent of overall size, whereas linear measurements are always strongly size-influenced. The significant correlation of this variable with the length of the frontal area does, however, suggest covariation between these two characters. Covariance in the controls of frontal area morphology is supported by the observation that the measures of frontal area proportion (f1 and j2) are correlated more strongly than with other variables. The correlation values of the palpebral lobe (c) with other variables

TABLE 21.—Eigenvalues and percentage of variance accounted for by each principal component in cranidial analysis of *Dikelocephalus* from the St. Lawrence Formation.

Principal component	1	2	3	4	5	6
Eigenvalue	4.88	0.92	0.11	0.06	0.02	0.01
Percentage variance	81.36	15.36	1.82	0.99	0.32	0.15
Cumulative percentage	81.36	96.72	98.54	99.53	99.85	100.00

are consistently lower than for cross-correlations either of f1 or j2 with other variables. This reflects the unique growth parameters of the eye (see above).

The overall importance of each principal component (i.e., how much of the total variation is accounted for by each principal component) is represented by the eigen value (Table 21). The contribution of each input variable to each principal component is also calculated and is referred to as the eigenweight (Table 22).

Principal components 1 and 2 account for the vast majority of variation within the sample (Table 21). Only 4% of the total variation is partitioned among the four other principal components. Each of the variables has a positive eigenweight for the first principal component. All variables, except the angle of divergence, have a high positive value of similar magnitude, suggesting that principal component 1 largely reflects overall size. However, the angle between principal component 1 and a hypothetical vector of isometry is 14.49°, which is statistically significant ($p<0.01$). Hence principal component 1 incorporates significant size-related shape change. This result is apparently due to the influence of one variable, the angular divergence of the facial suture (see below). The correlation ($p<0.05$) of the angular divergence of the facial suture with principal component 1 suggests slight positive allometry of this character. The contributions of variables to the other principal components is less uniform (Table 22). The angular variable has an extremely high loading on principal component 2, suggesting that this principal component largely reflects variance in this character. The length of the palpebral lobe (c) has a strong negative loading on principal component 3, suggesting that much of the variation of palpebral lobe length is accommodated in this axis. No other variables have strong loadings on principal component 3, but frontal area length (f1) shows a positive eigenweight. This may reflect the slight positive allometry of the length of the frontal area. A similar pattern has been observed in the proasaphiscid *Hundwarella personata* Reed (Hughes and Jell, 1992).

As principal component 1 accounts for 82% of the total variation and largely reflects overall size, size differences account for most of the variation within the sample. This is to be expected because the sample encompasses a wide range of holaspid instars. Principal components 2 to 6 show no obvious correlation with size. Each principal component reflects the influence of one or more of the variables, but there is no consistent pattern of covariance after size effects have been removed. The two linear variables related to the frontal area

morphology (f1, j2) show a weak pattern of covariance in their contribution to principal component 3, but they do not show covariance in their contributions to subsequent principal components (Table 21), nor does the angle of divergence of the facial suture covary with linear frontal area characters on principal component 3.

Plotting principal components against each other permits an assessment of the patterns of locality based variation. Bivariate plots of the first three principal components (Figures 31, 32) show that (1) each population occupies an approximately equivalent area of morphospace and (2) there is almost complete overlap among individuals from the four localities. When considering principal component 1 collection-related differences are less obvious in specimens that score low on that axis. This feature is partly a result of the increased measurement error at small sizes, although standardization of the data set should have reduced the effect of this error. Biological factors are also likely to promote similarity at small sizes because allometric differences may only become expressed among individuals of larger size. Hence scores on principal component 1 are not a reliable indicator of patterns of collection-related variation. However, as principal component 1 effectively removes differences in overall size, comparison of subsequent principal components is instructive in considering collection-based differences. The two regions of morphospace defined by individuals from Arcadia and North Freedom Bed 8 closely abut on principal components 2 and 3 (Figure 32), and individuals from the other two localities occupy regions of morphospace overlapping with both Arcadia and North Freedom Bed 8. There is a clinal pattern of variation between these localities. High scores on principal component 2 reflect high angular divergence of the facial suture, and high scores on principal component 3 reflect small eyes. Hence specimens

TABLE 22.—The relationship of each variable to each principal component is shown by the eigenweight in cranidial analysis of *Dikelocephalus* from the St. Lawrence Formation.

Principal component	eigenweight (directional cosine)					
	b1	f1	j2	< of div.	c	k
1	0.447	0.440	0.447	0.168	0.424	0.447
2	−0.106	0.028	0.014	0.966	−0.216	−0.093
3	0.111	0.327	0.335	−0.183	−0.851	0.107
4	0.279	−0.832	0.301	0.054	−0.133	0.345
5	0.306	0.077	−0.766	0.054	−0.176	0.529
6	0.778	−0.028	−0.109	0.020	−0.034	−0.617
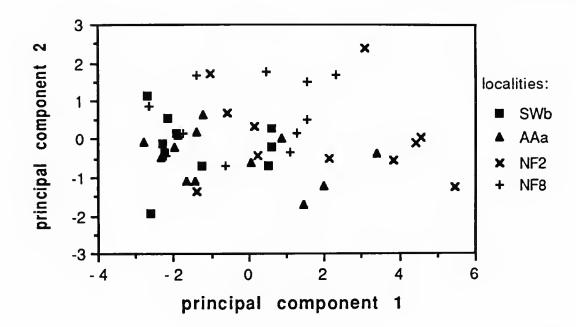
FIGURE 31.—Bivariate scatterplot of first two principal components in a sample of *Dikelocephalus* cranidia from four localities in the St. Lawrence Formation; n = 45. Localities are Stillwater (SWb), Arcadia Bed 18 (A Aa), North Freedom Bed 2 (NF2), and North Freedom Bed 8 (NF8).
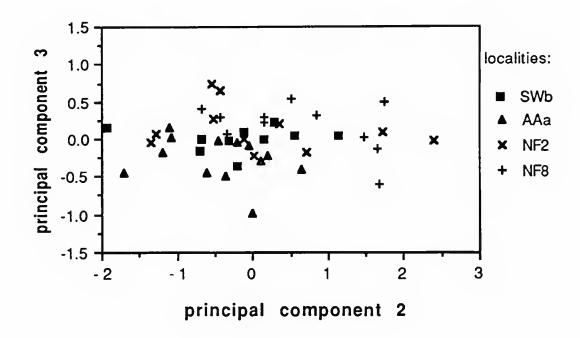
FIGURE 32.—Bivariate scatterplot of second and third principal components in a sample of *Dikelocephalus* cranidia from four localities in the St. Lawrence Formation. Data set as in Figure 31.

from Arcadia have relatively larger eyes and less divergent facial sutures than those from North Freedom Bed 8. These features are typical of the small holaspid growth stages of *Dikelocephalus*. Bivariate analysis has suggested a minor heterochronic shift affecting some characters within the Arcadia population. The pattern of variation in principal component analysis confirms this suggestion, and hence the small heterochronic shift can likely explain the clinal difference between the Arcadia and North Freedom Bed 8 populations.

Principal component 2 is strongly correlated with one variable, the divergence of the facial suture. This angular variable must be removed from the data set for comparisons between this analysis of *Dikelocephalus* and other multivariate

analyses of trilobites, because published principal component analyses of other trilobites rely only on linear measurements. Rerunning the PCA without the angluar variable yielded similar overall results, except that principal component 1 accounted for 95.40% of the total variance, and is isometric (the angle between principal component 1 and a hypothetical vector of isometry is 1.11°, which is not statistically significant ($p>0.89$)). Principal component 2 has loadings similar to principal component 3 of the previous analysis and a similar "shift" occurs between subsequent principal components.

Tunnel City Group Specimens: In order to assess the relationship of Tunnel City Group specimens to those of the St. Lawrence Formation a multiple group principal component

analysis was performed, with St. Lawrence Formation and Tunnel City Group specimens defined as different groups. Only nine Tunnel City Group specimens were sufficiently well preserved to be included in the analysis, and this small sample size limits the confidence that can be placed in the results of the principal component analysis of this group. The principal components calculated did, however, accord to a large extent with patterns expected a priori and were shown to be statistically similar to those in the St. Lawrence Formation collection.

As in the analysis of the St. Lawrence Formation collections, principal component 1 accounts for more than 80% of the total variation (81.9%) and principal component 2 accounts for most of the remaining variance (16.0%). The first three principal components account for 99.4% of the total variance. Patterns of character loading on the principal components were also similar to those in the St. Lawrence Formation analysis, the only notable difference being that the pattern of loading on principal components 4 and 5 were reversed. The width of the glabella (k) shows a positive loading on principal component 3, which may reflect the positive allometry of glabellar width noted in the bivariate analysis. Similarly, principal component 6 shows strong negative loading for occipital-glabellar length (b1) and positive loading for the glabellar width (k) again reflecting this allometry, although the total variance accounted for by this axis is so low that little confidence can be placed in the significance of this result.

Separate principal component analyses of St. Lawrence Formation and Tunnel City Group samples were compared with a principal component analysis of the pooled sample from both units. Chi-squared tests showed that the first three principal components are not significantly different between the pooled sample and 1, St. Lawrence Formation specimens ($p<0.99$, $p<0.98$, $p<0.99$ for differences between principal components 1 to 3 respectively); and 2, Tunnel City Group specimens ($p<0.64$, $p<0.21$, $p<0.13$ for differences between principal components 1 to 3 respectively). This suggests that similar patterns of variation occur among both St. Lawrence Formation and Tunnel City Group specimens.

Scores on the first three principal components in the pooled analysis (Figures 33, 34) show that the Tunnel City Group specimens lie within the range of variation shown by St. Lawrence Formation *Dikelocephalus*. Tunnel City Group specimens occupy a smaller volume of morphospace than do St. Lawrence Formation specimens, probably due to their smaller sample size. However, the specimens appear to plot on weakly defined arcs (Figures 33, 34). There may be a trend toward larger specimens showing lower scores on principal component 2 (Figure 33), but the small sample size prevents assessment of the significance of this trend. If confirmed by additional observations this pattern may reflect the unequal allometries of frontal area growth observed in the bivariate analyses of Tunnel City Group specimens (which was based on larger numbers of specimens). As frontal area length (f1)

increased allometrically at a faster rate than frontal area width (j2), the angular divergence of the suture would necessarily reduce, unless there was concomitant reduction in the width of the preocular incisure, which is not observed (Plate 9: Figures 1–5, 7–11).

Nonmetric Multidimensional Scaling

Multidimensional scaling calculates configurations of individuals in a specified number of multivariate dimensions, and then compares these configurations with the original association matrix of proximities. Where disparities exist the configuration is "stressed" to increase the goodness of fit between the configuration and the actual similiarities between individuals. This process is iterative. In this analysis three multivariate dimensions were selected and fifty iterations were computed. Stress values ranged from 14.06 at the first iteration to 1.07, an extremely low value of stress (Kruskal, 1964), at the sixth iteration, and remained constant thereafter. Considerable confidence can be placed in the resultant configuration, which was calculated on the basis of the 50th iteration because of the low stress value calculated in the last iterations.

Because MDS operates on an association matrix based on similarities, all cranidia of *Dikelocephalus* could be included in the analysis. The configuration of individuals in the cranidial nonmetric MDS analysis accords with the results of principal component analysis (Figures 35–37). The correlation between each of the first three multivariate axes calculated in the two techniques is high, indicating a close accordance of the results of principal component analysis and non-metric multidimensional scaling (pc1, MDS dimension 1 = –0.941; pc2, MDS dimension 2 = 0.944; pc3, MDS dimension 3 = –0.930). Dimension 1 of the MDS is largely size influenced, as expected.

The areas of morphospace defined by each locality all overlap, when dimensions 1 and 2 are plotted (Figure 35), but Tunnel City Group specimens and those from Arcadia (A Aa) and Stillwater (SWb) occupy separate area of morphospace in the plot of dimensions 2 and 3 (Figure 36). Specimens from Arcadia and those from North Freedom Bed 8 do not overlap in the plot of dimensions 2 and 3 (Figure 36), as in principal component analysis. These variations confirm the clinal pattern of variation documented by the bivariate analyses.

PYGIDIA.—Principal component analysis.

St. Lawrence Formation Specimens: A correlation matrix of the four input variables shows a significant relationship between all pairs (Table 23).

The high correlation coefficients between the intra-articulating pygidial length (z1) and both pygidial width (w) and axial length (y1) imply that the overall shape of the pygidium is rather constant among specimens. The intra-articulating spine length (z5) is less strongly correlated with the other characters. The data accord well with the results of bivariate studies (Table 18), which show variation in the spine
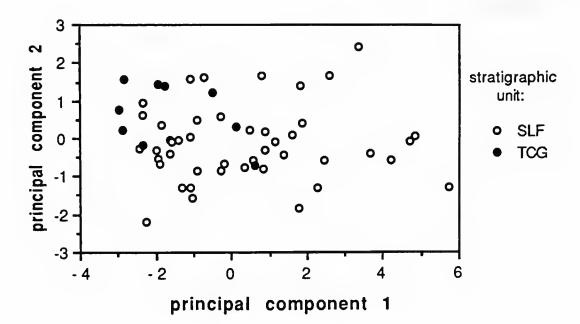
FIGURE 33.—Bivariate scatterplot of first two principal components in a sample of *Dikelocephalus* cranidia from the St. Lawrence Formation (SLF) and the Tunnel City Group (TCG); n = 54. All specimens considered in Figure 30 are included in the St. Lawrence Formation population. Tunnel City Group specimens are a pooled sample from five localities.
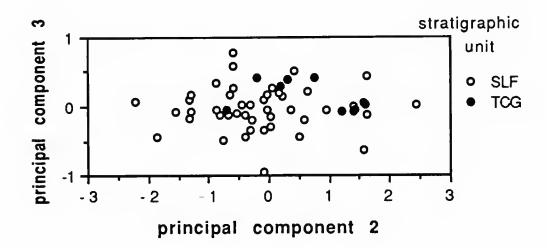
FIGURE 34.—Bivariate scatterplot second and third principal components in a sample of *Dikelocephalus* cranidia from the northern Mississippi Valley. Data set as in Figure 33.

TABLE 23.—Correlation matrix for pygidial characters of the multivariate sample of *Dikelocephalus* from the St. Lawrence Formation (n = 37). All values indicate statistical significance at the 99.9% confidence level.

	z1	z5	y1	w
z1		0.963	0.990	0.990
z5	0.963		0.950	0.950
y1	0.990	0.950		0.991
w	0.990	0.950	0.991	

TABLE 24.— Eigenvalues and percentage of variance accounted for by each principal component in pygidial analysis of *Dikelocephalus* from the St. Lawrence Formation.

Principal component	1	2	3	4
Eigenvalue	3.92	0.68	0.01	0.01
Percentage variance	97.94	1.62	0.22	0.21
Cumulative percentage	97.94	99.56	99.77	100.00
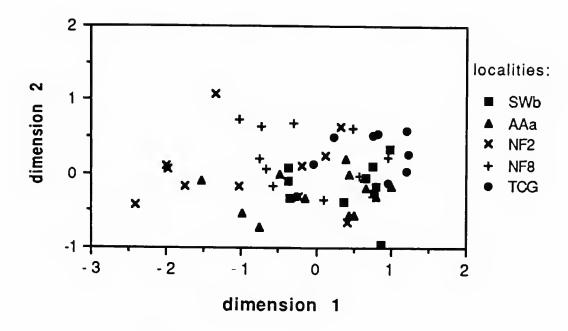
FIGURE 35.—Bivariate scatterplot of first two multivariate dimensions calcultated by nonmetric multidimensional scaling of *Dikelocephalus* cranidia from the northern Mississippi Valley. Data set as in Figure 33.
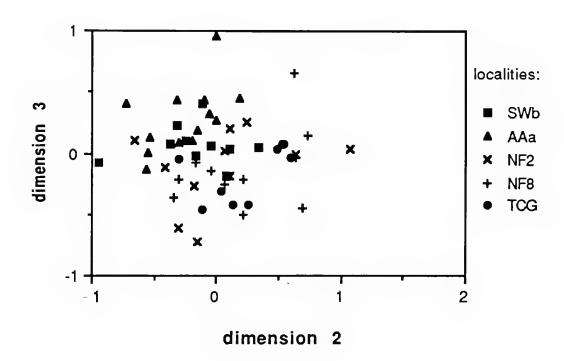
FIGURE 36.—Bivariate scatterplot of second and third multivariate dimensions calculated by nonmetric multidimensional scaling of *Dikelocephalus* cranidia from the northern Mississippi Valley. Data set as in Figure 33.

length to be a principal source of morphological variation within St. Lawrence Formation *Dikelocephalus*.

As in the analysis of the cranidium, principal component 1 explains most of the variation (Table 24). Less than 2% is accounted for by the other principal components. The overwhelming importance of principal component 1 might swamp other styles of variation, yielding subsequent principal components that account for a tiny proportion of the total variance, with patterns of eigenweight loadings that may not be significant. However, several observations that principal components 2 to 4 do represent significant patterns of variation

in *Dikelocephalus*. Firstly, the angle between principal component 1 and a hypothetical vector of isometry (0.47°) is not significant ($p < 0.97$), suggesting that principal component 1 reflects only differences in overall size within the sample. This is supported by the observation that the eigenweights of principal component 1 are all positive and of similar magnitude (Table 25).

Intra-articulating spine length ($z5$) shows a strong positive loading on principal component 2, whereas other variables show negative eigenweights but of smaller magnitude. Subsequent principal components reflect the influence of one or more
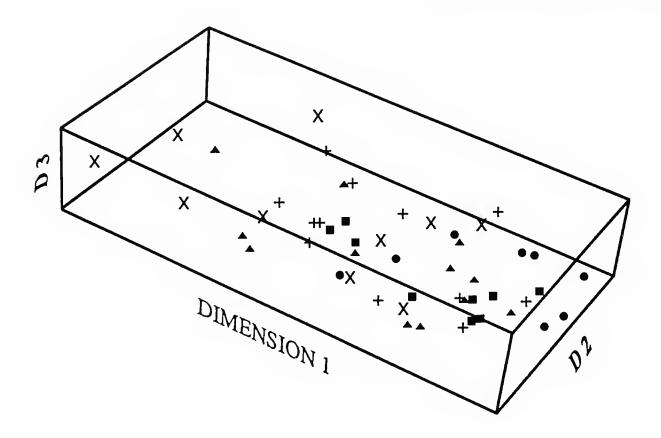
FIGURE 37.—Trivariate scatterplot of first three multivariate dimensions calculated by nonmetric multidimensional scaling of *Dikelocephalus* cranidia from the northern Mississippi Valley. Data set as in Figure 33.

of the variables, but there is no consistent pattern of covariance after size effects have been removed. The length of the axis (y1) has strong positive loading on principal component 3, whereas the pygidial width (w) shows negative loading, suggesting that relatively wide forms tend to have a shorter axis.

Bivariate plots of the first three principal components (Figures 38, 39) show that there is complete overlap among individuals from the four localities. Several of the smaller specimens from Arcadia (A Aa) show high scores on principal component 2, reflecting the extremely long spines present at this locality. Other specimens from this locality, however, show scores that fall within the range of values present among individuals from all other localities. There are no grounds for recognizing two morphs within the Arcadia population, for abundant intracollection variation in other pygidial characters from this locality is not linked with the pattern of variation in spine length.

Tunnel City Groups Specimens: In order to assess the relationship of Tunnel City Group specimens with those of the

TABLE 25.—The relationship of each variable to each principal component is shown by the eigenweight in pygidial analysis of *Dikelocephalus* from the St. Lawrence Formation.

Principal component	eigenweight (directional cosine)			
	z1	z5	y1	w
1	0.503	0.493	0.502	0.502
2	-0.137	0.856	-0.356	-0.348
3	-0.223	0.046	0.774	-0.587
4	-0.821	0.146	0.148	0.532

St. Lawrence Formation a multiple group principal component analysis was performed, with St. Lawrence Formation and Tunnel City Group specimens defined as different groups (Figures 40, 41). Only fourteen Tunnel City Group specimens were sufficiently well preserved to be included in the analysis, and this small sample size limits the confidence that can be placed in the results of the principal component analysis of this group (Figure 42). However, as in the analysis of the cranidia the principal components calculated did accord to a large extent with patterns expected a priori, based on the results of the bivariate analysis.

Principal component 1 accounted for 98.0% of the total variation in the pooled sample. This slight increase in the amount of variation accounted for by principal component 1 compared to that of the St. Lawrence Formation specimens suggests that St. Lawrence Formation and Tunnel City Group samples show very similar patterns of variation. Principal component 1 is again isometric ($p < 0.96$). The first two principal components account for 99.4% of the total variance. Patterns of character loading on the principal components were also very similar to those in the St. Lawrence Formation analysis, the only notable difference being that the polarity of loading on principal component 4 was reversed in the pooled analysis.

Separate principal component analyses of St. Lawrence Formation and Tunnel City Group samples were compared with a principal component analysis of the pooled sample from both units. Chi-squared tests showed that the first three principal components are not significantly different between the pooled sample and St. Lawrence Formation specimens
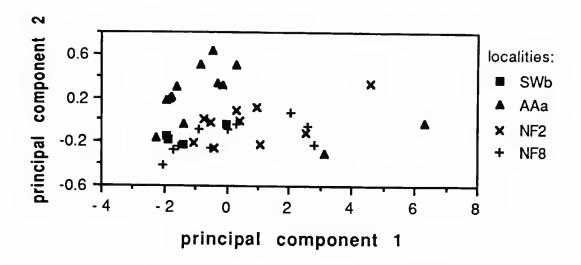
FIGURE 38.—Bivariate scatterplot of first two principal components in a sample of *Dikelocephalus* pygidia from four localities in the St. Lawrence Formation; n = 37. Localities are Stillwater (SWb), Arcadia Bed 18 (A Aa), North Freedom Bed 2 (NF2), and North Freedom Bed 8 (NF8). Exaggeration on y axis ×3.
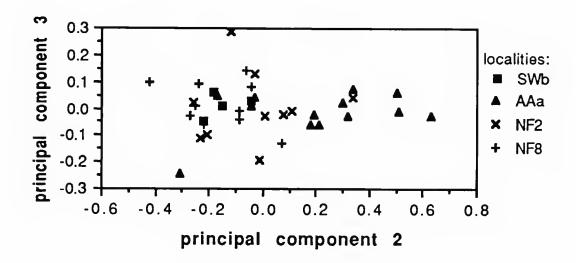

FIGURE 39.—Bivariate scatterplot of second and third principal components in a sample of *Dikelocephalus* pygidia from four localities in the St. Lawrence Formation. Data set as in Figure 38.

TABLE 26.—Eigenvalues and percentage of variance accounted for by each principal component in pygidial analysis of *Dikelocephalus* from the Tunnel City Group.

Principal component	1	2	3	4
Eigenvalue	3.96	0.26	0.01	0.01
Percentage variance	99.00	0.62	0.32	0.06
Cumulative percentage	99.00	99.62	99.94	100.00

TABLE 27.—The relationship of each variable to each principal component is shown by the eigenweight in pygidial analysis of *Dikelocephalus* from the Tunnel City Group.

Principal component	eigenweight (directional cosine)			
	z1	z5	y1	w
1	0.500	0.499	0.499	0.501
2	0.564	−0.490	−0.507	0.430
3	−0.025	−0.715	0.698	0.041
4	0.657	0.013	0.081	−0.750

($p<0.99$, $p<0.95$, $p<0.88$ for differences between principal components 1 to 3 respectively). The Tunnel City Group does (Table 26), however, show significant differences from the pooled sample in principal components 2 and 3 ($p<0.99$, $p<0.01$, $p<0.01$ for differences between principal components 1 to 3 respectively). These differences are reflected in the different eigenweights on principal components 2 and 3 in the analysis of the Tunnel City Group collection (Table 27).

The consistent pattern of strong positive loadings on principal component 1, which is isometric ($p = 1.00$), is indistinguishable from the patterns in the pooled sample and the St. Lawrence Formation sample (Table 27). In the pooled analysis specimens from the Tunnel City Group overlap with those from the St. Lawrence Formation, although their group centroid is displaced from the mean centroid of the St. Lawrence Formation specimens. Loadings on principal components 2 and 3 differ significantly from those of the pooled sample. Within the Tunnel City Group all variables have strong loadings on principal component 2 (unlike the St. Lawrence
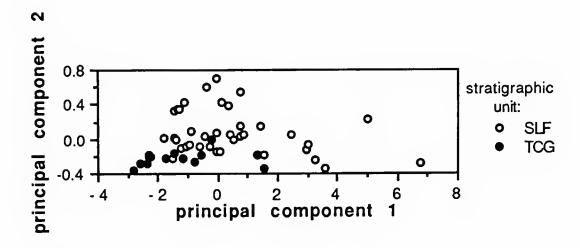
FIGURE 40.—Bivariate scatterplot of first two principal components in a sample of *Dikelocephalus* pygidia from the northern Mississippi Valley; n = 51. All specimens considered in Figure 38 are included in the St. Lawrence Formation population. Tunnel City Group specimens are a pooled sample from 7 localities. Exaggeration on y axis ×3.
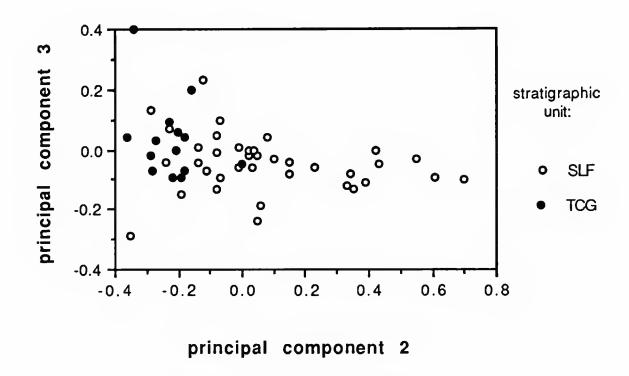
FIGURE 41.—Bivariate scatterplot of second and third principal components in a sample of *Dikelocephalus* pygidia from the northern Mississippi Valley. Data set as in Figure 40.

Formation, where only z5 loads strongly on this axis) but the polarities of the loadings differ. Pygidial length (z1) and width (w) have positive eigenweights, but axial (y1) and intra-articulating spine length (z5) both load negitively. Scores on principal component 2 correlate with those on principal component 1 (Figure 40), such that small specimens score relatively highly on principal component 2, although one large specimen from Excelsior forms a distinct outlier. This pattern suggest ontogenetic control of pygidial shape, with smaller specimens having relatively short axes and spines, in marked contrast to the pattern in the St. Lawrence Formation collection alone. A similar pattern of ontogenetic variation was suggested by loadings on principal component 2 in the cranidial analysis, again pointing to likely differences in growth patterns between the faunas from the two stratigraphic units.

Nonmetric Multidimensional Scaling

As in the cranidial analysis nonmetric multidimensional scaling was used to assess the specimen interrelationships. Three multivariate dimensions were selected and fifty iterations were computed. Stress values ranged from 12.78 at the first iteration to 0.17 at the tenth iteration, and remained constant thereafter. Because 0.17 is an extremely low value of stress (Kruskal, 1964), considerable confidence can be placed in the resultant configuration, which was calculated on the basis of the fiftieth iteration.

The configuration of individuals in the cranidial nonmetric MDS analysis accords very closely with the results of principal component analysis (Figures 43–45). The correlation between each of the first three multivariate axes calculated in the two
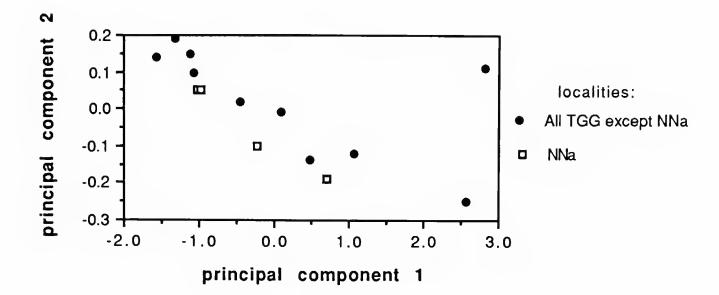
FIGURE 42.—Bivariate scatterplot of first two principal components in a sample of *Dikelocephalus* pygidia from the Tunnel City Group; n = 14. Specimens from Newton (NNa), Vernon Co., Wisconsin, are identified. Other Tunnel City Group specimens are from six localities including Freeburg (FG) and Hell Hollow (HW), Houston Co., Minnesota, Excelsior (EX), Richland Co., Bean Hollow (BN), and Genoa (GA), Vernon Co., Wisconsin, and Lansing (LSb), Allamakee Co., Iowa. Exaggeration on y axis ×5.

techniques is high, indicating a close accordance of the results of principal component analysis and non-metric multidimensional scaling (pc1, MDS dimension 1 = –0.999; pc2, MDS dimension 2 = 0.981, pc3, MDS dimension 3 = –0.503). Dimension 1 of the MDS is largely size-influenced, as size is the principal morphological variation within the sample.

The areas of morphospace defined by specimens from each collection all overlap when dimensions 1 and 2 are plotted (Figure 43). Tunnel City Group specimens plot separately from those from Stillwater (SWb) in the plot of dimensions 2 and 3 (Figure 44), but this likely reflects the small sample size from this locality. Some specimens from Arcadia form a distinctive group, separated from the main cluster of points. This pattern was also seen, though to a lesser extent, in the principal component analysis. As this group largely reflects variation in the length of the pygidial spine it is not considered likely to be of taxonomic significance, for reasons discussed above.

Dimension 3 appears to reflect features that distinguish some Tunnel City Group specimens from most St. Lawrence Formation specimens, but substanitial overlap exists between the two.

DISCUSSION

Trilobite populations generally display a wide size range, partly due to their molting habit. In consequence, principal component 1 accommodates a huge proportion of the total variance in the sample. This pattern has been noted in many arthropod taxa, both fossil and living (e.g., Eldredge, 1972, 1973; Andrews et al., 1974; Ashton and Rowell, 1975; Temple, 1975b; Solignac et al., 1990; Bruton and Owen, 1988). Most of the variance is accounted for by principal component 1, even in trilobites showing variation caused by such taphonomic factors as tectonic deformation (Hughes and Jell, 1992).
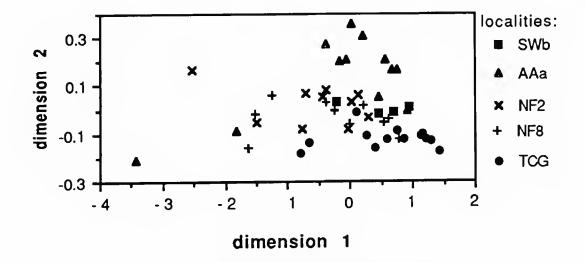
FIGURE 43.—Bivariate scatterplot of first two multivariate dimensions calcultated by nonmetric multidimensional scaling of *Dikelocephalus* pygidia from the northern Mississippi Valley. Data set as in Figure 40. Exaggeration on y axis ×3.
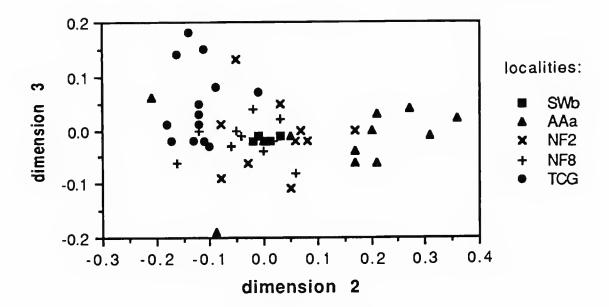
FIGURE 44.—Bivariate scatterplot of second and third multivariate dimensions calculated by nonmetric multidimensional scaling of *Dikelocephalus* pygidia from the northern Mississippi Valley. Data set as in Figure 40.
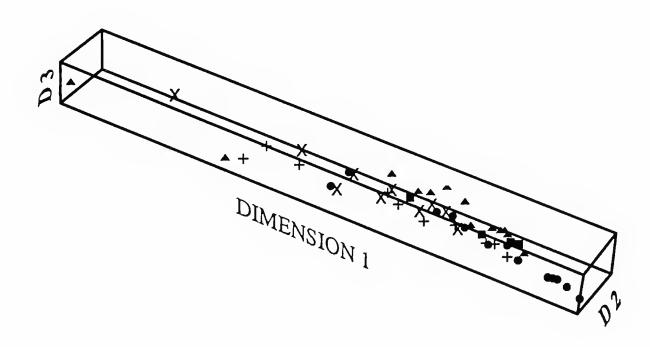
FIGURE 45.—Trivariate scatterplot of first three multivariate dimensions calculated by nonmetric multidimensional scaling of *Dikelocephalus* pygidia from the northern Mississippi Valley. Data set as in Figure 40.

No consistent pattern of clustering occurs within the sample. There is no evidence that any locality contained more than one morph of *Dikelocephalus* and broad overlap occurs between specimens from all localities. Of all specimens, those from Arcadia and the Tunnel City Group are the most widely separated, indicating that these groups have the greatest difference in morphology. *Dikelocephalus* from the Tunnel City Group show overlap with those from North Freedom (NF2, NF8) and Stillwater (SWb). In most cases intracollection variation is as great as the variation between collections. The results of principal component analysis is consistent with the results of the bivariate analyses.

Three different approaches (nominal/ordinal character analyses, bivariate analyses, and multivariate analyses) have been used to examine morphological variation within *Dikelocephalus*. The results of each approach are consistent, and suggest that all St. Lawrence Formation *Dikelocephalus* should be treated as a single morphospecies, *Dikelocephalus minnesotensis* Owen. The species shows a high degree of intraspecific variability.

Systematic Paleontology

Class TRILOBITA Walch, 1771

Subclass LIBRISTOMA Fortey, 1990

Order ASAPHIDA Salter, 1864; emended Fortey, 1990

Superfamily DIKELOCEPHALACEA Miller, 1889; emended Ludvigsen, Westrop, and Kindle, 1989

Family DIKELOCEPHALIIDAE Miller, 1889; emended Ludvigsen, Westrop, and Kindle, 1989

REMARKS.—The presence of large eyes located close to the cranidium is synapomorphic for the family Dikelocephalidae (Ludvigsen, Westrop, and Kindle, 1989), but genera within the group are poorly defined. Westrop (1986) argued that the presence of an extended cephalic doublure is synapomorphic for an advanced group of within the Dikelocephaliidae, including *Dikelocephalus, Briscoia, Elkia, Walcottaspis,* and *Oseolia.*

Genus *Dikelocephalus* Owen, 1852

EMENDED DIAGNOSIS.—Dikelocephalid trilobites with a single pair of posterolateral pygidial spines; pleural segments are equally divided or have expanded propleural bands.

TYPE SPECIES.—*Dikelocephalus minnesotensis* Owen (1852:574), from the St. Lawrence Formation, Fairy Glen, Washington County, Minnesota.

REMARKS.—Westrop's (1986) diagnosis of *Dikelocephalus* stressed the absence of the anterior border furrow in large holaspids, the presence of a single pair of posterolateral spines, and the subequal division of the pleurae. Several of these characters are present in other dikelocephalids. *Osceolia* possesses a pair of posterolateral spines and shows border effacement in larger specimens. Many *Briscoia* show unequal division of the pleurae (Palmer, 1968). Unlike all saukiids and *Briscoia,* in which the unequal division represents the swelling of the opisthopleurae, unequal division of the pleurae in *Dikelocephalus* is due to propleural expansion. This feature distinguishes *Dikelocephalus* from all other advanced dikelocephalids *(Briscoia, Elkia, Walcottaspis,* and *Oseolia),* which have either expanded opisthopleurae or highly modified pleural furrows. *Dikelocephalus* is characterized by the possession of posterolateral pygidial spines and pleurae that are equally divided or have expanded propleurae. In gross morphology *Walcottaspis* resembles *Dikelocephalus* more closely than any other dikelocephalid. *Walcottaspis* has fewer pygidial segments than *Dikelocephalus,* and if the posterolateral spine of *Dikelocephalus* is associated with the first pygidial segment (see above), then the last thoracic segment of *Walcottaspis* may

be homologous with the first pygidial segment of *Dikelocephalus.* The small palpebral lobes, long frontal area, and, presumably, larger number of thoracic segments of *Walcottaspis* may indicate a peramorphic condition with respect to *Dikelocephalus,* but until a phylogenetic anlaysis of the dikelocephalids is completed this suggestion will remain speculative.

Dikelocephalus minnesotensis Owen, 1852

FIGURES 46, 47; PLATES 1–8, 10: FIGURES 14, 15, PLATE 11

Dikelocephalus minnesotensis Owen, 1852:574 [in part], pl. 1: figs. 1, 2 (not fig. 10), pl. 1a: figs. 3, 6.—Mackie, 1859:189, fig. 4 [reproduces Owen's fig. 1].—Hall, 1863:138, pl. 9: figs. 5–10, pl. 10: figs. 10–12, pl. 11: figs. 1, 3, 4 [species described and figured].—Sardeson, 1896:95 [discusses horizon].—Walcott, 1914:369, pl. 60: figs. 1–8, pl. 61: figs. 1–3, 5–7, pl. 62: figs. 4–6, pl. 66: fig. 1 [genus redescribed, species listed].—Raymond, 1924:434.—Walter, 1926:192, pl. 10: figs. 1–7 (not figs. 8, 9) [redescribes species, specimens from Iowa illustrated].—Ulrich and Resser, 1930:20, pl. 1: figs. 6–8, pl. 3: fig. 1 [redescribes species].—Kobayashi, 1936:169 [cited as generic type].—Stauffer and Thiel, 1941:26, 30, 46, 133, 160, 169, 171, 201, 205, 212, 215, 222 [lists occurrence in Minnesota].—Shimer and Shrock, 1944:623, pl. 261: figs. 7, 8 [describes species].—Raasch, 1951:142, 148 [synonymizes most of Ulrich and Resser, 1930, species, reducing the genus to eight species].—Nelson, 1951:784, pl. 110: figs. 14, 17 [redescribes and illustrates two species of the genus]; 1956:172, 179 [discusses horizon].—Lochman, 1956:468 [mentions occurrence in Iowa].—Berg, Nelson, and Bell, 1956:19 [discusses distribution in Minnesota].—Harrington, 1959:O56, fig. 42, no. 10 [figures hypostome].—Lochman, 1959:O254, fig. 190, no. 1a–c, fig. 191, no. 3 [cites *D. minnesotensis* Owen as generic type species].—Hughes, 1991:913, fig. 1 [discusses intraspecific variation and figures complete specimen]; 1993:1–49, pl. 1–7 [discusses distribution and taphonomy].—Labandeira and Hughes, 1994: 492, pl. 1: figs. 1–17 [biometric analysis of type suite].

Ogygia minnesotensis (Owen).—Chapman, 1856:275.

Dicellocephalus minnesotensis Owen.—Miller, 1877:216 [listed].—Lesley, 1889:198, fig. 1 [gives location and reproduces Owen's figures].

Dikellocephalus minnesotensis Owen.—Whitfield, 1882:187, pl. 3: fig. 1 [species described and a pygidium illustrated].

Dikelocephalus barretti Ulrich and Resser, 1930:57, pl. 16: figs. 1–7.—Raasch, 1935:312 [listed].—Twenhofel, Raasch, and Thwaites, 1935:1713, 1727 [listed].—Raasch, 1951:141.

Dikelocephalus beani Ulrich and Resser, 1930:37, pl. 19: figs. 1, 2.

Dikelocephalus brevis Ulrich and Resser, 1930:55, pl. 1: figs. 1–5, pl. 14: figs. 1, 2.—Raasch, 1935:312 [listed]; 1939:98 [listed].

Dikelocephalus declivis Ulrich and Resser, 1930:56, pl. 15: figs. 8, 9.

Dikelocephalus edwardsi Ulrich and Resser, 1930:48, pl. 9: figs. 1–5.—Raasch, 1939:99 [listed].

Dikelocephalus gracilis Ulrich and Resser, 1930:41, pl. 9: fig. 6, pl. 10: fig. 4, pl. 11: figs. 1, 2, pl. 12: figs. 1, 2, pl. 13: figs. 1, 2.—Raasch, 1935:312 [listed].—Twenhofel, Raasch, and Thwaites, 1935:1713 [listed].—Raasch, 1939:15, 25, 98, 104 [stratigraphic position listed in relation to aglaspidids].—Schuldt, 1941:396 [discusses occurrence in Iowa].—Shimer and Shrock, 1944:623, pl. 261: figs. 3, 4 [describes species].

Dikelocephaus granosus Ulrich and Resser, 1930:58, pl. 6: figs. 8–10.—Twenhofel, Raasch, and Thwaites, 1935:1727 [listed].—Raasch, 1939:24, 30, 98, 101, 103, 107, 108 [listed].

Dikelocephalus halli Ulrich and Resser, 1930:24, pl. 18: figs. 1–7.

Dikelocephalus hotchkissi Ulrich and Resser, 1930:23, pl. 2: figs. 1–3, pl. 3: fig. 5.

Dikelocephalus inaequalis Ulrich and Resser, 1930:35, pl. 19: figs. 3–6.— Raasch, 1935:312 [listed]; 1939:101, 103 [listed]; 1951:139, 142, 148.

Dikelocephalus intermidius Ulrich and Resser, 1930:26, pl. 3: figs. 3, 4.

Dikelocephalus juvinalis Ulrich and Resser, 1930:30, pl. 22: fig. 10.

Dikelocephalus marginatus Ulrich and Resser, 1930:49, pl. 15: figs. 1–7.—Raasch, 1939:101 [listed]; 1951:142, 148.—Nelson, 1956:172, 179 [discusses horizon].—Berg, Nelson, and Bell, 1956:19, 20 [discusses distribution in Minnesota].

Dikelocephalus norwalkensis Ulrich and Resser, 1930:52, pl. 21: figs. 11–21.—Raasch, 1935:312 [listed].—Twenhofel, Raasch, and Thwaites, 1935:1713, 1734 [listed].—Raasch, 1939:101, 104, 108 [listed].—Shimer and Shrock, 1944:623, pl. 261: figs. 1, 2 [describes species].—Raasch, 1951:138, 141.

Dikelocephalus orbiculatus Ulrich and Resser, 1930:29, pl. 4: figs. 1–4.— Raasch, 1939:104, 105 [listed].

Dikelocephalus ovatus Ulrich and Resser, 1930:44, pl. 13: figs. 3–7.—Raasch, 1935:312 [listed].

Dikelocephalus oweni Ulrich and Resser, 1930:32, pl. 5–7, pl. 8: figs. 1–3.—Raasch, 1935:312 [listed].—Twenhofel, Raasch, and Thwaites, 1935:1713, 1724 [listed].—Raasch, 1939:101 [listed].—Shimer and Shrock, 1944:623, pl. 261: fig. 12 [describes species].—Twenhofel, 1945:633, pl. 88: fig. 3 [describes new specimens from Galesville].—Raasch, 1951:141, 148.—Nelson, 1956:172, 179 [discusses horizon].—Berg, Nelson, and Bell, 1956:19, 20 [discusses distribution in Minnesota].—Westrop, 1986:29, pl. 3: figs. 1–4 [describes specimens from Alberta].

Dikelocephalus postrectus Ulrich and Resser, 1930:52, pl. 20: figs. 1, 2.—Twenhofel, Raasch, and Thwaites, 1935:1732 [listed].—Stauffer and Thiel, 1941:30, 40 [discusses horizon].—Raasch, 1951:141, 149.

Dikelocephalus raaschi Ulrich and Resser, 1930:38, pl. 8: fig. 4, pl. 10: figs. 1–3.—Rasetti, 1952:892 [discussion of median suture].—Harrington, 1959:067 [discusses presence of median suture].

Dikelocephalus retrorsus Ulrich and Resser, 1930:47, pl. 14: figs. 6–8, pl. 15: figs. 1, 2.—Rasetti, 1952:892 [discussion of median suture].

Dikelocephalus subplanus Ulrich and Resser, 1930:45, pl. 14: figs. 3–5.— Twenhofel, Raasch, and Thwaites, 1935:1727 [listed].—Rasetti, 1952:892 [discussion of median suture].—Harrington, 1959:067 [discusses absence of median suture].

Dikelocephalus thwaitesi Ulrich and Resser, 1930:54, pl. 21: figs. 1–10.— Raasch, 1951:140, 141, 147, 149.—Nelson, 1951:783, pl. 110: figs. 13, 19; 1956:172, 177, 178, 180, 181 [discusses horizon].—Berg, Nelson, and Bell, 1956:19 [discusses distribution in Minnesota].

Dikelocephalus weidmani Ulrich and Resser, 1930:37, pl. 17: figs. 2–6.— Raasch, 1935:312 [listed].

Dikelocephalus wiltonensis Ulrich and Resser, 1930:28, pl. 17: figs. 7–9.

Dikelocephalus wisconsinensis Ulrich and Resser, 1930:40, pl. 9: figs. 7–10.—Twenhofel, Raasch, and Thwaites, 1935:1727 [listed].—Nelson, 1956:172 [discusses horizon].

Dikellocephalus raaschi Ulrich and Resser.—Stubblefield, 1936:413 [discusses median suture].

Dikellocephalus subplanus Ulrich and Resser.—Stubblefield, 1936:413 [discusses median suture].

Dikelocephalus 'gracilis ovatus' Raasch, 1939:96, 98 [listed, not discussed].

Dikelocephalus cf. *weidmani* Ulrich and Resser.—Raasch, 1939:101 [listed].

Dikelocephalus regalis Ulrich and Resser.—Ulrich and Resser, 1940:40 [nomenclatural change replacing *D. oweni* Ulrich and Resser, 1930, which is preoccupied by *D. oweni* Billings, 1865).—Hupé, 1953:186(166), fig. 163, no. 2 [figured].

Dikelocephalus sp. indet. Grant, 1965:110, pl. 13: figs. 1, 2 [figures specimens from Montana].

Dikelocephalus cf. *norwalkensis* Ulrich and Resser.—Ostrom, 1965:20 [listed].

Dikelocephalus sp. Winston and Nichols, 1967:75, pl. 10: fig. 8 [illustration of a cranidium from Texas].

Dikelocephalus winona (?) Ostrom, Davis, and Cline, 1970:101, 123 [cites species as occurring at Mazomanie, etymology of this species unknown, it has no prior history, no formal description, and is therefore a nomen nudum].

Dikelocephalus sp. 2 Stitt, 1971:17–18, pl. 5: fig. 20 [describes cranidium from Oklahoma].

TYPE MATERIAL.—USNM 17863 (Plate 11: Figure 18; Labandeira and Hughes, 1994, pl. 1: fig. 17), from Fairy Glen, Stillwater (SWa), Washington County, Minnesota, is here selected as lectotype (original of Owen, 1852, pl. 1: fig. 1, counterpart of pygidium; Ulrich and Resser, 1930, pl. 1: fig. 8). USNM 447020 (Plate 11: Figure 17; original of Owen, 1852, fig. 1, cranidium; Ulrich and Resser, 1930, pl. 1: fig. 6; Labandeira and Hughes, 1994, pl. 1: fig. 1) is a paralectotype. Of Owen's (1852, pl. 1: fig. 2, pl. 1a: figs. 3, 6) other figured material of *D. minnesotensis,* only paralectotype USNM 447021 has been located (Owen, 1852, pl. 1a: fig. 6). Type material of species subsumed in this analysis include the specimens figured by Ulrich and Resser (1930, pls. 1–19, pl. 20, figs. 1, 2, pl. 21, pl. 22: fig. 10). Those specimens include USNM 71736a,b; USNM 71738–71742; MPM 18656–18674; USNM 71747; USNM 71752–71755; USNM 71756a,b,c; USNM 58600; USNM 58596; USNM 58602; USNM 58594; USNM 58597; USNM 58598; USNM 71759; USNM 71744; USNM 71745; USNM 58606; USNM 58603; USNM 58604; USNM 71743; USNM 58612; USNM 71749; USNM 58599; MPM 18675; USNM 71748; MPM 18676–18680; USNM 71806; MPM 18682–18685; USNM 71799 (incorrectly reported as USNM 71879 by Ulrich and Resser, 1930:104); USNM 17865; MPM 11179; USNM 71746; USNM 58607; USNM 71800–71802; MPM 11186; MPM 11904; USNM 71803; USNM 71804; MPM 11176; MPM 18686–18688; USNM 71750; USNM 71751; USNM 71805; MPM 18690; MPM 9557–9560; USNM 71808–71811; USNM 71807; USNM 58609; USNM 58610; USNM 72676–72686; MPM 18691; USNM 58623; USNM 72695–72713; USNM 58601.

OTHER MATERIAL.—Major holdings include (approximate number of specimens in parentheses): American Museum of Natural History (70); British Museum (Natural History) (10); Cincinnati Museum of Natural History (10); Field Museum of Natural History (90); Geological Survey of Canada (20); Museum of Comparative Zoology, Harvard University (40); Natural History Museum of Los Angeles County (40); Milwaukee Public Museum (700); Sauk County Historical Museum (30); Science Museum of Minnesota (160); University of Cincinnati (25); University of Bristol (10); University of California, Berkeley (5); University of Minnesota Paleontology Collection (100); United States Geological Survey, Denver (20); United States National Museum of Natural History (500); University of Wisconsin Geology Museum, Madison (1000). Additional specimens are held in the collections of the University of Wisconsin, Eau Claire; the University of Wisconsin, Milwaukee; and the Bristol City Museum.

EMENDED DIAGNOSIS.—As for genus, because only one species is sufficiently known to warrant recognition.

DESCRIPTION.—Dorsal shield rounded, length (sag.) to width (tr.) ratio about 1.3, isopygous. Pleural region broad, axis

narrow and convex. Largest individuals estimated to be at least 40 cm long.

Glabella widest (tr.) just posterior of S1 (sag.); lateral margins subparallel anterior of S1; with rounded anterolateral corners and straight to slightly curved anterior margin. S1 transglabellar, forming posteriorly directed arch, connecting with or terminating just before axial furrow; shallow and broad (sag.) in axial quarter, deeply incised, sigmoidal distally. S2 straight, deepest distally, crossing one-quarter to one-third of glabellar width (tr.), running transverse to slightly obliquely backwards. S3 straight, running obliquely forwards and inwards, one-fifth of glabellar width (tr.), deepest at midlength (tr.), absent in largest holaspids. Shallow intercalated furrows run subparallel to and just anterior of occipital furrow across distal quarter of L1; other intercalated furrows run subparallel to and just posterior of S1, S2, and S3, across one-fifth of glabellar width (tr.). Occipital furrow straight or with slight sigmoidal flexure, deepest at one-quarter of glabellar width (tr.), broader and shallow in axial third. Occiptial ring with low ridge that runs parallel to and just anterior of posterior margin. Intercalated furrow runs subparallel to and posterior of occipital furrow across distal quarter of occipital ring. Median occipital tubercle sometimes present. Cephalic axial ornament variable; pustules most strongly developed axially, elongate on anterior margin of glabella, absent from holaspids with occipital-glabella lengths longer than about 2.5 cm. Axial furrow strongly developed laterally, shallow in front of glabella; anterolateral pits weakly developed.
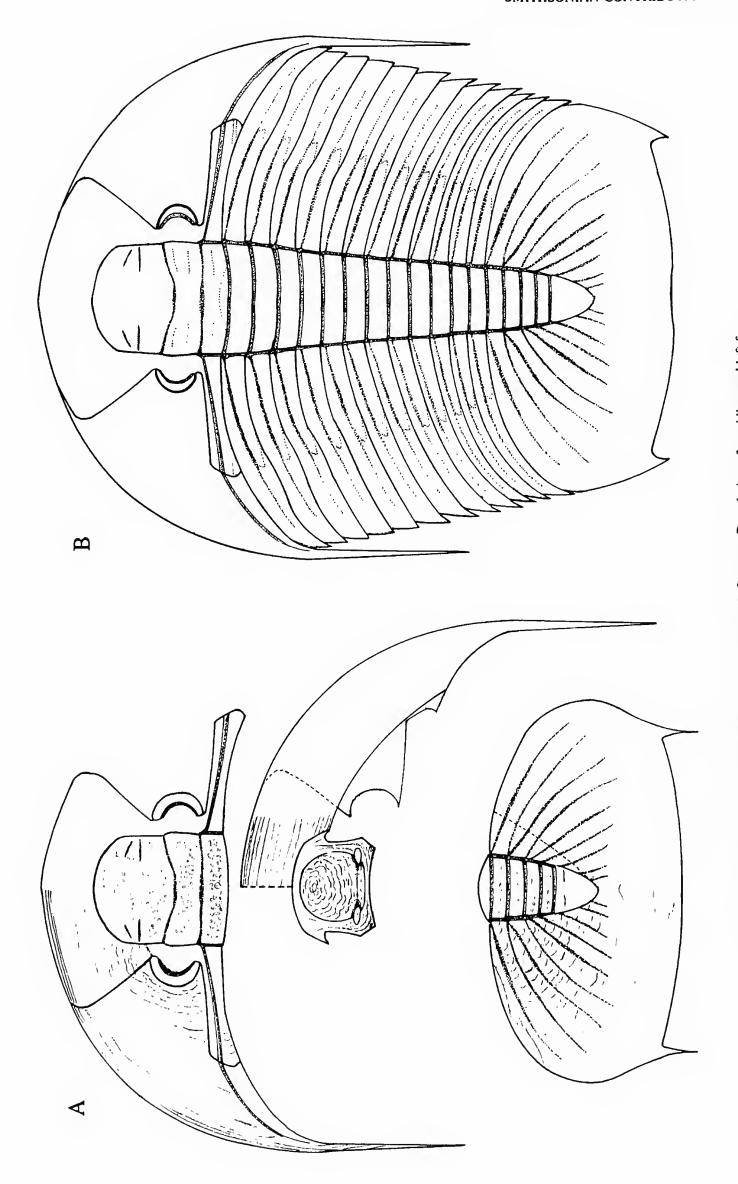
Frontal area broad, flat to downsloping, one-third to one-half of occipital-glabellar length, one and one-half to twice occipital width (tr.). Anterior margin rounded to slightly angular axially; border short (sag.), low where developed. Two to five transverse terrace ridges developed on border. Anterior border furrow crescentic, weakly to well-defined. Where well-defined, eight or more unevenly spaced pits developed along its length (tr.). Caeca, broad, running across preglabellar field between anterior pits, dying out in border furrow. Terrace lines confined to posterior half of preglabellar field (sag.), inosculate, steeper slopes facing outwards, becoming granular preoccipitally. Dorsal cephalic suture marginal, or nearly so in preglabellar area, then sweeps inward at an angle of 15° to 50° to sagittal axis toward faint eye ridge. Fixigena narrowest (tr.) opposite L2, widest opposite (tr.) midpoint of L1 (sag.) (widest opposite S1 (exsag.) in some stratigraphically lower specimens); intraocular fixed cheek flat or inflated against palpebral furrow, slopes gently toward axial furrow (tr.); palpebral furrow strongly incised; palpebral lobe width (tr.) one-quarter to one-half of occipital length (sag.), lobe length decreases realtive to glabellar length through ontogeny. Lobe length (exsag.) up to half occipital-glabellar length (sag.) in small holaspids, up to quarter of occipital-glabellar length in large holaspids. Posterolateral border area narrow (exsag.), expanding distally, spatulate, equal in width (tr.) to occipital lobe. Postocular suture transverse, subparallel to posterolateral

margin. Posterior marginal furrow deeply incised, sigmoidal, converging with axial furrow just posterior of S1. Shallow furrows run parallel to posterior marginal furrow along abaxial portion of posterior lateral border area. Terrace ridges developed on distal portion.

Free cheeks arcuate. Border flat, rising steeply adaxially towards flat ocular platform; lateral border furrow shallow when present; posterior border furrow sigmoidal, curving posteriorly along base of genal spine; genal spine frequently longer (exsag.) than cranidium, narrow (tr.), gently curved outward; ocular incisure arcuate, bounded adaxially by shallow arcuate furrow and raised marginal flange. Terrace ridges on dorsal surface prominent, steeper slopes face outwards, straight to slightly sinuous abaxially, running slightly oblique to margin, inosculate to granular on ocular platform, curving adaxially along posterior margin. Doublure wide, extending about nine-tenths of distance from margin to ocular incisure, with flexure in its anterior portion that accommodates the anterior edge of the hypostome. Median suture may be present or free cheeks may be fused. Doublure curves upward adaxially, remaining close beneath dorsal surface. Terrace ridges on doublure straight, steeper slopes facing outward; about 17 present, most densely developed at margins.

Hypostome (labrum) subquadrangular, wider (tr.) than long (sag.); median body large, oval, inflated anteriorly; anterior lobe convex in small holaspids, round; posterior lobe short (sag.), wide (tr.). Median furrow pit-like abaxially, shallow axially; maculae oval, prominent within medial furrow in small holaspids, absent in larger specimens; pit-like furrows are developed at posteriolateral margin of posterior lobe; border furrow weakly incised; anterior border upturned, short (sag.) axially, widens (sag.) laterally into wide (tr.) anterior wings; anterior wings elongated, curving posteriorly towards dorsal surface of cephalon where they terminate in rounded tip; lateral border triangular, widest (tr.) opposite midpoint of posterior lobe. Posterior border lip-like, gently arched anteriorly in axial portion. Terrace ridges on median body inosculate, steep sided. Terracing on anterior lobe concentric about a point on sagittal axis just anterior of the midpoint of the lobe. Terraces loop around maculae, transverse on posterior lobe. Terracing on lateral border straight to sinuous, cuestaform, steep slopes facing adaxially.

Twelve thoracic segments present in some holaspids; axial ring pustulated in smaller specimens. Median tubercle occasionally present; anterior margin of pleurae straight for short distance from axial furrow (tr.), curving posteriorly abaxial of fulcrum; anterior facet broad, showing petaloid ornament; posterior margin sigmoidal in anterior segments, more smoothly curved in posterior segments; pleural tip blunt in anterior, elongate and spine-like in posterior segments; pleural furrow sigmoidal in anterior, smoothly curved in posterior segments, deeply incised adaxially, shallow abaxially, reaching almost to tip of pleura; propleura and opisthopleura of equal length (sag.) at midpoint of pleurae. Opisthopleura may show

FIGURE 46.—Reconstruction of *Dikelocephalus minnesotensis* Owen: A, Dorsal view of cranidium and left free cheek; ventral view of left free cheek and hypostome; and dorsal view of pygidium of small holaspid, showing details of surface ornamentation, approximately ×2. B, Dorsal shield of large holaspid, approximately ×0.25–0.5.
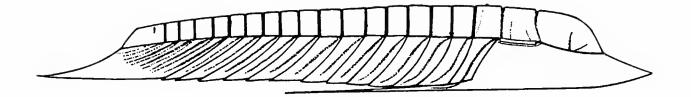
FIGURE 47.—Reconstruction of large holaspid of *Dikelocephalus minnesotensis* Owen, lateral view, approximately ×0.3–0.5.

granulation or inosculate terracing near axial furrow. Terrace ridges transverse on anterior facet of propleurae. Low ridge runs transversely across opisthopleura from posterior border. Ridge originates about one-fifth of width (tr.) of pleurae from axial furrow, terminates about two-fifths of pleural width (tr.) in a swollen node just posterior of pleural furrow. Doublure extends adaxially at least as far as opisthopleural node. Terraces on doublure straight, subparallel to sagittal axis, steep slopes facing outwards.

Pygidium transversely subelliptical with pair of marginal spines originating posterolaterally; marginal spines in small holaspids relatively longer than in large holaspids; posterior margin straight to gently curved; postaxial emargination present in some larger specimens. Axis convex, one-half to four-fifths of pygidial length (sag.) in most specimens, longer in stratigraphically lower specimens; with four rings and terminal piece; a poorly defined fifth ring of two transverse pits is occasionally present; ring furrows deeply impressed distally, shallow medially; ridge arches anteriorly from posterior border of first axial ring, occupying medial three-quarters of ring width (tr.) and extending across one-third to one-half of ring length (sag.); ridge may also be present in second and subsequent axial rings; first and second axial rings pustulated in smaller specimens; terminal piece may be inflated, posterior margin rounded to bullet-shaped; terracing on terminal piece inosculate, continuous from pleural region; postaxial ridge narrow and tubular where present. Pleural platform flat, abaxial margin of platform corresponding to faint paradoublural line; pleural region beyond pleural platform concave, margin flat; interpleural furrows narrow, first pair deeply incised adaxially, shallow distally; pleural furrows long, deeply incised, similar extent to interpleural furrows. Four to five pleura present, fifth poorly defined. First pleura contains equally divided pro- and opisthopleura. Subsequent pleurae show equal division of pleurae or a reduction in the length (exsag.) and width (tr.) of opisthopleurae relative to propleurae. High relief on terrace ridges, crescentic on pleural platform, inosculate to straight toward margins, steeper slopes facing outwards. Petaloid terraces developed on articulating facet of first pleura. Doublure wide extending inwards two-thirds of pleural width (tr.); marginal rim occasionally present, ridgelike. Doublure curving upwards, close beneath dorsal surface. Doublure terrace ridges straight to sinuous, relief high, steeper slopes

facing outwards; 22–28 present, most densely distributed along adaxial margin.

OCCURRENCE.—Southern Alberta: *Illaenurus* Zone, Mistaya Formation (limestone). Southwestern Montana: *Illaenurus* Zone, Sage Member, Snowy Creek Formation (limestone). Central Texas: *Saukiella norwalkensis* Subzone, *Saukia* Zone, San Saba Member, Wilberns Formation (limestone). South-central Wisconsin, southeastern Minnesota, and northeastern Iowa: *Saukia* Zone, Reno Member and upper part of Mazomanie Formation (Tunnel City Group) (sandstone), and St. Lawrence Formation (fine sandstones and shales). Southcentral Oklahoma: *Saukiella serotina* Subzone, *Saukia* Zone, Signal Mountain Formation (limestone). Also recorded from Colorado (shale) and Nevada (limestone), stratigraphic details poorly known.

REMARKS.—Specimens of *Dikelocephalus minnesotensis* illustrated by Owen (1852) all appear to have positive relief and superficially appear to have been parts. Those original specimens of *D. minnesotensis* which have been located (Owen, 1852, pl. 1: fig. 1, pl. 1a: fig. 6) are all counterparts. This discrepancy is explained by Owen's (1852) use of a special "medal-ruled on steel" engraving technique.

Several specimens from the Tunnel City Group, described as *Dikelocephalus freeburgensis* by Feniak (in Bell, Feniak, and Kurtz, 1952, pl. 35: fig. 4, pl. 38: fig. 4a–e; herein illustrated as Plate 10: Figures 3, 17–19) show marked morphological differences from St. Lawrence Formation *Dikelocephalus minnesotensis*, particularly in the pygidium. Statistical analysis suggests that differences may occur in growth relationships between Tunnel City Group and St. Lawrence Formation *Dikelocephalus*. However, other *Dikelocephalus* from the Tunnel City Group are morphologically close to *D. minnesotensis* and are considered conspecific with that taxon (e.g., *Dikelocephalus postrectus*). The relationships of Tunnel City Group *Dikelocephalus* cannot be resolved until more complete collections from single bedding planes are available. Unfortunately, *Dikelocephalus* is not common in the Tunnel City Group (Hughes, 1993, fig. 1). Until more Tunnel City Group specimens are recovered, and the relationships within the dikelocephalid clade better known, *D. freeburgensis* should be restricted to its type and figured specimens. Retention of this name (rather than synonymy with *D. minnesotensis*) maintains taxonomic stability and affirms that insufficient evidence is currently available to evaluate the status of these specimens.

Morphological Variation in *Dikelocephalus*

INTRODUCTION

Inadequate appreciation of the morphological plasticity within *D. minnesotensis* resulted in extensive taxonomic subdivision of the species by previous authors. It is demonstrated here that all St. Lawrence Formation *Dikelocephalus* constitute a single, highly plastic morphospecies. It is now possible to evaluate possible causes for the pattern of variation seen in *D. minnesotensis,* and assess the significance of this variation for broader paleobiological questions.

VARIATION CONTROLS

Within *Dikelocephalus minnesotensis* morphological variation can be loosely partitioned into growth-related and population-related components.

GROWTH-RELATED VARIATION.—There are two recognized causes of shape change during growth (Gould, 1966). First, some growth relationships are controlled by size/volume developmental constraints, which automatically require shape change if the same function is to be performed in both small and large individuals. Second, shape variations may be related to changes in life mode, such as the transition from pelagic to benthic habit (Speyer and Chatterton, 1989).

Morphometric analyses suggest that the shapes of holaspid cephala and pygidia were modified progressively and gradually through the ontogeny of *Dikelocephalus,* as growth relationships are always continuous. These trends probably reflect size/volume developmental constraints. As the change in volume relative to size diminished between late holaspid molts shape change between each molt became less marked. Hence characters that are controlled by size or volume factors vary more in early ontogeny than in late ontogeny. Strong allometric relationships in *Dikelocephalus* show a curve that flattens and becomes rectilinear at large sizes. This is consistent with a size/volume developmental control. Non-isometric rectilinear relationships among holaspids of *D. minnesotensis* may represent the expression of a constant allometric control that is curvilinear at smaller sizes, but has flattened out before holaspid growth commences. Recovery of pre-holaspid growth stages is needed to test this hypothesis.

Dikelocephalus minnesotensis shows a high degree of ontogenetically-controlled variation during the holaspid period compared to other trilobites (Hughes, 1991). Part of the marked variation in *Dikelocephalus* results from the high degree of allometry. The extension of significant allometry into the holaspid stage suggests that somatic development was delayed relative to overall size in *D. minnesotensis* (and in some other large trilobites). It is not clear to what extent size variations between trilobite species reflect environmental rather than genetic controls, as ecophenotypic variation in overall size is common within trilobites (Sheldon, 1988). However, the presence of large specimens in all lithotypes within the northern Mississippi Valley suggests that the large size of *Dikelocephalus* was not related to a specific environment.

Slight variations in the initial growth conditions between individuals will be compounded through ontogeny into major morphological differences (McNamara, 1986). Hence it is not surprising that the most obvious intraspecific variations within the heterolithic facies concern those features showing the strongest allometry. Some intercollection differences are due to intraspecific heterochronic shifts, which may be facultative (i.e., environmentally-triggered) and do not necessarily imply genotypic differences (Pachut, 1989).

POPULATION-RELATED VARIATION.—*Paleoenvironmental and Paleoecological Influences on Variation:* Is developmental plasticity in *D. minnesotensis* a direct result of the paleoenvironmental setting? Species living in nearshore, low diversity associations often show unusual patterns of variation, reflecting a biologically stressful habitat (Bretsky and Lorenz, 1970; Eldredge, 1974; McKinney, 1986; Pachut, 1989). Facies analysis (Hughes, 1990) shows that, apart from possible brief periods of exposure, marine conditions persisted throughout the deposition of the St. Lawrence Formation. Although it was perhaps subject to exposure, the paleoenvironment does not appear to be environmentally heterogeneous. Only three major facies have been identified in a region over 30,000 km^2. The generic diversity of trilobites and other invertebrates in the St. Lawrence Formation is similar to that found in other Upper Cambrian biofacies (Ludvigsen and Westrop, 1983b; Hughes, 1993) and does not represent a depleted, low-diversity fauna. Although inadequate study of intraspecific variation in Cambrian trilobites makes accurate estimation of species diversity impossible at present, it is likely that the diversity of the northern Mississippi Valley Sunwaptan is similar to that estimated in contemporaneous subtidal shelf deposits from elsewhere in North America (Westrop, 1988). This is because the within-locality generic diversity of trilobites of collections from the St. Lawrence Formation (Hughes, 1993) is similar to that of localities from other Upper Cambrian shelf biofacies (see Westrop, 1986, 1988).

Cambrian nearshore environments commonly show both sedimentary homogeneity and normal biotic diversity relative to more distal shelf environments (compare facies associations reported by Westrop, 1989, with those of Hughes, 1990). There is no evidence of unusually high environmental stress in the northern Mississippi Valley. Indeed, contemporaneous offshore carbonate facies are characterized by peritidal conditions, emergence, and storm-related deposition. These facies may well have been more stressful than sites nearer the exposed craton.

Stitt (1971, 1975) suggested that species appearing near the bases of biomeres show greater intraspecific variation than those higher in the biomere. He considered that this was due to progressively increased intraspecific competition and narrowing of niche widths following adaptive radiation. The range of

Dikelocephalus lies near the top of the Ptychaspid Biomere. According to Stitt's model the genus should show little intraspecific variation. The results of this analysis show this to be incorrect. Longacre (1970) demonstrated a degree of intraspecific variation in trilobites from the base of the Ptychaspid Biomere that appears similar to that shown in *Dikelocephalus*. It has been claimed that Stitt's (1971, 1975) model of adaptive radiation has not been supported by morphometric analysis of species within the Ptychaspid Biomere (Ashton and Rowell, 1975; Eldredge, 1977). Ashton and Rowell (1975) stated that levels of intraspecific variation remained consistent throughout the biomere. However, their interpretation is erroneous because the authors mistakenly interpreted variation in specimen size as a measure of intraspecific variability. No conclusions can yet be made about the relationship between morphological plasticity and evolution within biomeres.

The large size of *D. minnesotensis*, *Saukia*, *Tellerina*, and some aglaspidids (Hesselbo, 1987) relative to that of other contemporaneous arthropods, suggests that these organisms pursued *K*-selective strategies that are associated with stable environmental conditions and high diversity (Gould, 1977; Pachut, 1989). Both geological and biologic evidence suggest that the environment during accumulation of the St. Lawrence Formation was no more stressful than at contemporary off-shore shelf sites. Hence, it is unlikely that morphological plasticity in *Dikelocephalus* resulted from unusual environmental or ecological conditions.

Genetic Basis: Size-independent intraspecific variation has two principal causes: (1) genetic polymorphism among local populations, each of which are developmentally-canalized (in the sense of Johnson, 1981); and (2) a genetically flexible (i.e., poorly-canalized) genotype, producing ecophenotypic variation in response to local environmental influences (Johnson, 1981). The mosaic pattern of variation in *Dikelocephalus* suggests either flexible developmental response to local environmental conditions or random interpopulational variations. Both possiblitities suggest that *Dikelocephalus* had a flexible developmental genome, rather than a series of genetically canalized polymorphs.

The position of the eye and length of the post-axial pygidial border are ontogenetically invariant in *D. minnesotensis*. Hence temporal trends in these characters cannot be explained in terms of heterochronic character displacement within the species. Too little is known of the stratigraphic controls on these characters to warrant speculation on the nature (gradual or otherwise) of the temporal trends. However, the intrapopulational variation of many characters equals their temporal and morphoclinal variation and the pattern of variation in *D. minnesotensis* may represent net morphological stasis (in the sense of Eldredge and Gould, 1972).

The pattern of variation in *Dikelocephalus* may be characteristic of other Cambrian trilobite species. Early Cambrian olenellids are difficult to classify at the low taxonomic levels

because "genera intergrade among the large number of olenellid species known" and that "this difficulty in supraspecific discrimination represents an important aspect of evolutionary systematics of trilobites that has ... not ... been fully appreciated" (Palmer and Halley, 1979:66). Similar observations were made by Fritz (1992:10). This observation of remarkable plasticity in olenellids was apparently first made by Kiaer (1917:86) who, when discussing convergent patterns of evolution in the olenellid genera *Callavia*, *Kjerulfia*, *Wanneria*, and *Holmia*, commented that there was much specialization crossing in this group (also see Stubblefield, 1936:413). McNamara (1983, 1986, 1991) has demonstrated considerable heterochrony in Cambrian trilobites and shown that the number of thoracic segments in holaspids may vary among species of Cambrian trilobites, whereas the number is constant at the generic, familial, and even sub-ordinal levels in many post-Cambrian taxa. He considered this early developmental plasticity to represent developmentally flexible genomes in Cambrian species. Ramsköld (1991) interpreted this trend as an example of Rosa's rule which is the tendency for evolution to go from variation of a character in primitive members of a clade to fixation in advanced members. A similar observation of morphological plasticity in early members of a trilobite clade was recorded within the encrinurids (Ramsköld, 1991). Similarly, the contrasting patterns of variation in dorsoventral file number in some Ordovician *Calyptaulax* and Devonian *Phacops* may provide another example of Rosa's rule (Ramsköld, 1991). Other evidence that may support the idea of early plasticity is the presence of out-of-phase genetic programs in some Cambrian trilobite species (Zhang and Clarkson, 1990) and morphometric analysis of the diversification of trilobites by Foote (1990, 1991). Foote has shown that from the Early Cambrian to the Late Ordovician there was a progressive change in species discreteness and that the "average species in the Ordovician is actually less similar to its nearest-neighbor than is the average Cambrian species" (Foote, 1990:378).

Recent analysis of the morphological diversity of trilobites (Foote, 1991) based on outline analysis of the shape of the cranidium has shown increasing diversity (as measured by morphospace occupied) of trilobites from the Cambrian to the mid-Ordovician. If Cambrian and Ordovician taxa are compared, there is a striking change in the pattern with which morphospace is occupied. Ordovician taxa occupy morphospace more discontinuously than Cambrian taxa, resulting in discrete Ordovician higher taxa characterized by stable synapomorphies, which have long been been recognized by trilobite systematists. Cambrian taxa occupy morphospace in a more continuous fashion which explains the difficulty of imposing trilobite higher level systematics on Cambrian trilobites, which has been called the ptychoparioid problem (Lochman, 1947; Rasetti, 1955; Schwimmer, 1975; Blaker, 1986; Fortey, 1990; Babcock, in press). It has recently been recognized that the Order Ptychoparida is based on symple-

siomorphies and hence is an artificial group (Fortey and Chatterton, 1988; Fortey, 1990). Several Cambrian taxa have been now been identified as primitive sister taxa of advanced groups that expanded rapidly in the Ordovician. However, the difficulties of Cambrian trilobite systematics are broader than the problem of rampant paraphyly in the Cambrian, because Cambrian trilobite taxa are less distinctive from one another regardless of phylogenetic position or taxonomic rank (Foote, 1990). The pattern of mosaic variation documented here in *Dikelocephalus* mimics those patterns seen at higher taxonomic levels in other Cambrian trilobites. Character instability and mosaic variation in Cambrian taxa may be a general feature at all taxonomic levels, as preliminary analysis of levels of homoplasy in Cambrian taxa suggests (Hughes, 1992; Babcock, in press). Increased developmental regulation, with concomitant decreased morphological plasticity and homoplasy may have important implications for patterns of evolution within the trilobites (McNamara, 1986; Hughes, 1991), also in other arthropods (Gould, 1991), and possibly other groups involved in the Cambrian radiation (Gould, 1989). Uncertainty concerning the degree of disparity in Cambrian arthropods (Briggs and Fortey, 1989; Gould, 1991; Briggs, Fortey, and Wills, 1992; Foote and Gould, 1992) reflects the fact that the fossil record of soft-bodied forms is highly incomplete, which inhibits detailed analysis of diversification patterns. Studies of diversification must focus on taxa that have a good Paleozoic fossil record (such as trilobites, echinoderms, and brachiopods) and address questions of the morphological plasticity within the context of well substantiated phylogenetic analyses.

Conclusions

This work is the first detailed documentation of the variation within a Cambrian trilobite species. Many characters previously considered to be "species-specific" are shown to vary intraspecifially. Future taxonomic studies of trilobites must provide a full account of morphological variability within species. Analysis of size-independent variations are essential before assessments of the taxonomic significance of individual characters can be made. Heterochronic studies may not take sufficient account of intraspecific variation, resulting in the misinterpretation of phenotypic variation as evolutionary trends. Special caution is needed when assessing evolutionary relationships between taxa when the sample size is small. Detailed analysis of intraspecific variation in large samples provides an important basis for understanding the relationships between closely-related taxa. Studies of holaspid ontogenetic variation provides evidence of phylogenetic relationships between sister taxa by defining character polarities and identifying heterochronic shifts. A combination of morphometric and phylogenetic approaches that permit assessment of the evolution of character complexes is essential before much progress can be made in understanding evolutionary processes within Paleozoic invertebrates.

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Plates

PLATE 1

Dikelocephalus minnesotensis Owen: St. Lawrence Formation; heterolithic facies.

FIGURE 1.—USNM 443599; dorsal shield; locality unknown, ×1.

FIGURE 2.—Private collection of Gerald Gunderson; dorsal shield with cranidium missing, ×2. North Freedom Bed 2 (NF2), Sauk County, Wisconsin.

FIGURE 3.—USNM 447014; thorax, pygidium, and posterior of cephalon, ×1. North Freedom, probably Bed 2 (NF2), Sauk County, Wisconsin.

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PLATE 2

Dikelocephalus minnesotensis Owen: from Stillwater, Washington County, Minnesota (SWb). St. Lawrence Formation; heterolithic facies. All specimens are internals of composite molds, unless otherwise stated. Details of collections and localities are listed in Hughes (1993).

FIGURE 1.—SMM 34-2087; cranidium, with large palpebral lobes, ×2.

FIGURE 2.—SMM 34-2029a; cranidium, with large palpebral lobes and median tubercle, ×2.

FIGURE 3.—SMM 34-2024; cranidium, showing pustulation and terrace ridges on border, ×2.

FIGURE 4.—SMM 34-2097; free cheek, lacking median suture, ×1.

FIGURE 5.—SMM 34-2092b; ventral view of hypostome, with maculae, ×2.

FIGURE 6.—SMM 34-2025a; cranidium, showing prominent median tubercle, ×1.5.

FIGURE 7.—SMM 34-2017b; cranidium, with relatively smaller palpebral lobes and short frontal area, ×1.

FIGURE 8.—SMM 34-2018a; fragment of larger cranidium, note that the termination of the palpebral lobe is posterior of S2 furrow, ×1.

FIGURE 9.—SMM 34-2094; ventral view of hypostome, lacking clear maculae, ×2.

FIGURE 10.—SMM 34-2043a; free cheek, ×1.

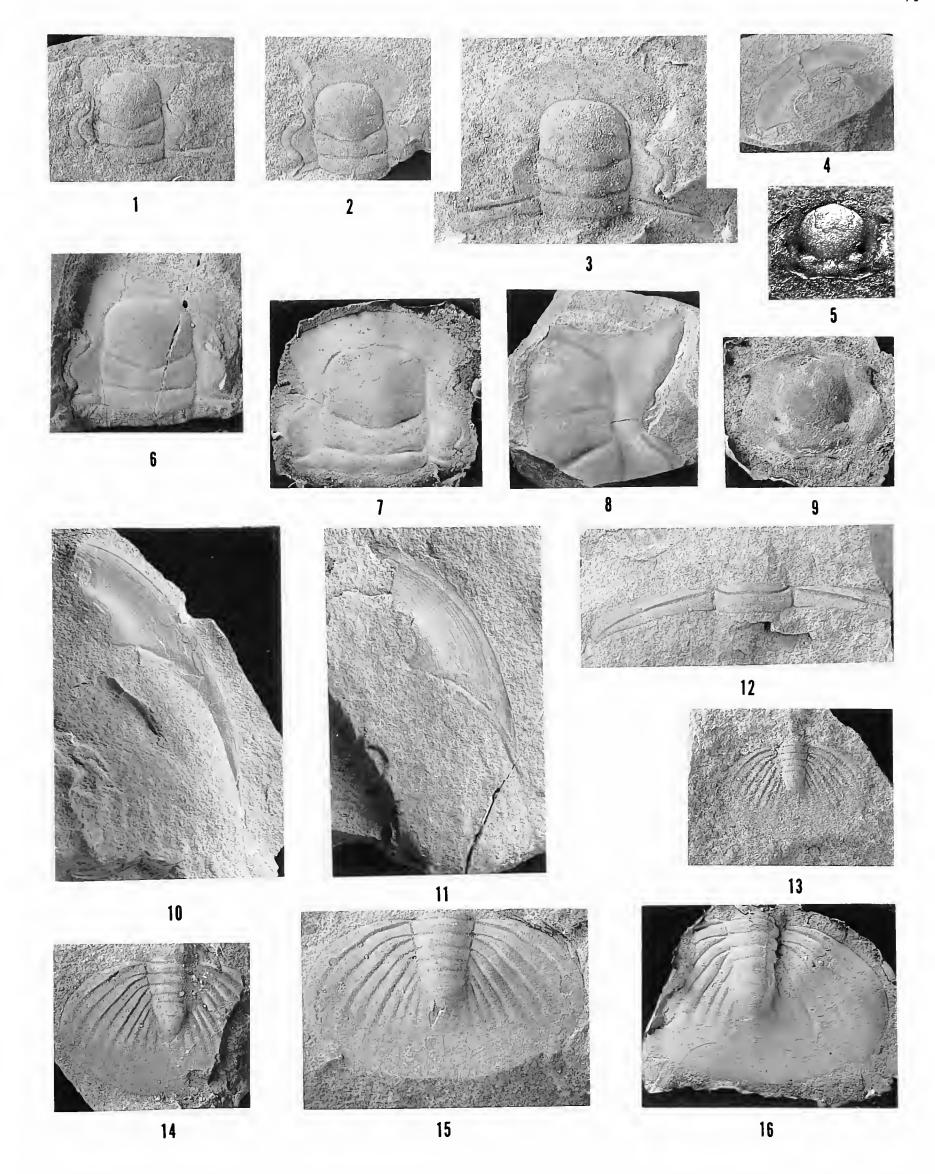FIGURE 11.—SMM 34-2019a; free cheek, ×1.

FIGURE 12.—SMM 34-2053; thoracic segment with medial axial pustule, ×2.

FIGURE 13.—SMM 34-2089; pygidium, with long post-axial region and equally divided pleurae, ×2.

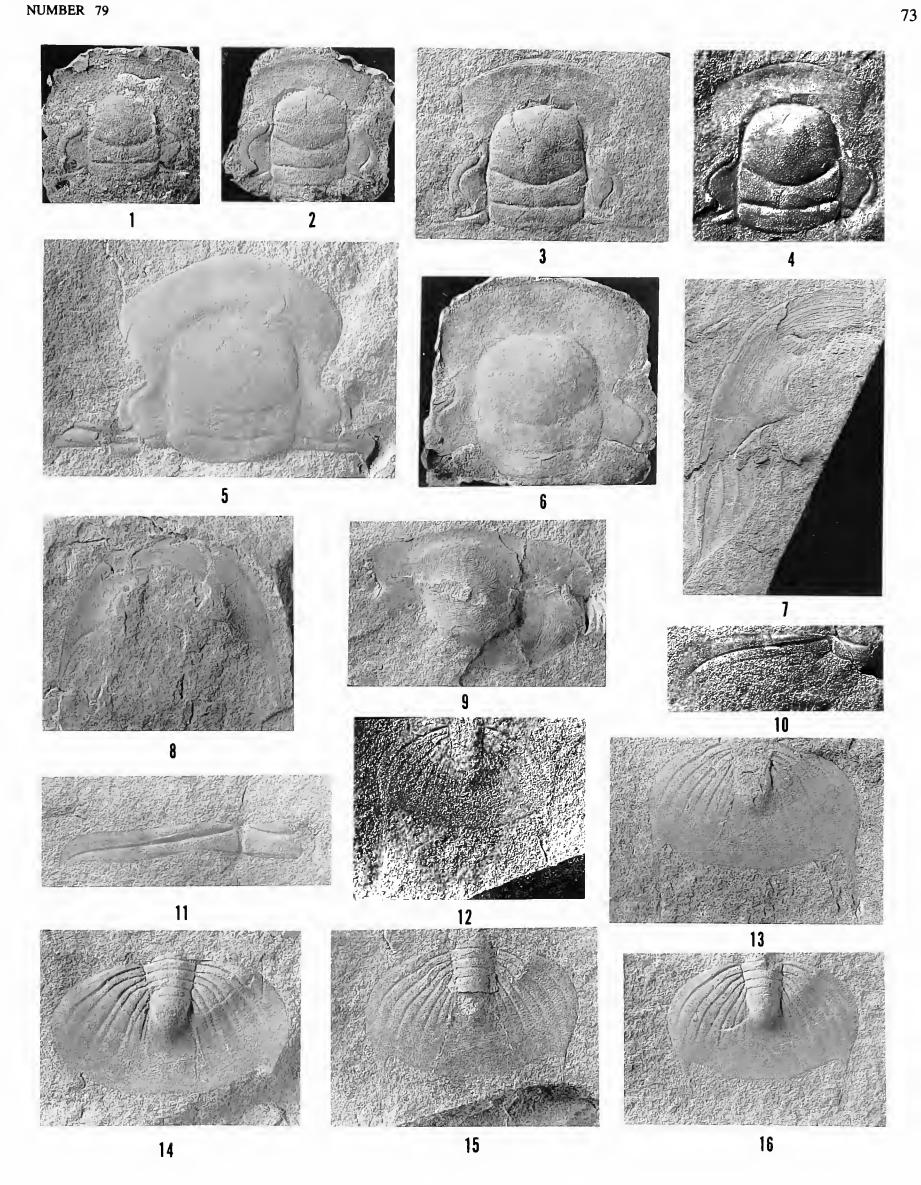FIGURE 14.—SMM 34-2080; pygidium, ×1.5.

FIGURE 15.—SMM 34-2081; pygidium, ×1.5.

FIGURE 16.—SMM 34-2126a; pygidium, with slightly unequally divided pleurae, ×1.

PLATE 3

Dikelocephalus minnesotensis Owen: from Arcadia, Trempealeau County, Wisconsin (A Aa). St. Lawrence Formation; heterolithic facies.

FIGURE 1.—UW 4006-364; cranidium, latex of counterpart, with the unusually large early holaspid palpebral lobes characteristic of this locality, ×2.

FIGURE 2.—UW 4006-369; cranidium, latex of counterpart, with the unusually large early holaspid palpebral lobes characteristic of this locality and low anlge of divergence of the anterior branch of the facial suture, ×2.

FIGURE 3.—UW 4006-293; cranidium, with features typical of this locality, pustulated and with small median tubercle, ×1.5.

FIGURE 4.—UW 4006-372; cranidium, pustulated and with median tubercle, ×1.

FIGURE 5.—UW 4006-338; cranidium, ×1.

FIGURE 6.—UW 4006-359; cranidium, latex of counterpart, with palpebral lobes of similar dimension to similarly sized holaspid cranidia from other localities, ×0.75.

FIGURE 7.—UW 4006-308a; free cheek, with median suture, ×1.

FIGURE 8.—UW 4006-286; yoked free cheeks, lacking median suture, ×1.

FIGURE 9.—UW 4006-294; ventral view of hypostome, with terrace ridges, ×1.

FIGURE 10.—UW 4006-280; thoracic segment, from posterior part of thorax showing ornament on adaxial part of pleurae, ×1.

FIGURE 11.—UW 4006-282; thoracic segment, from anterior part of thorax showing ornament on adaxial part of pleurae, ×1.

FIGURE 12.—UW 4006-324a; pygidium, with extremely long spines characteristic of this locality and equally divided pleurae, ×1.5.

FIGURE 13.—UW 4006-320; pygidium, showing pleural abnormality on third pleural segment on right side of pygidium, ×1.5.

FIGURE 14.—UW 4006-327a; pygidium, with unequally divided pleurae, ×1.5.

FIGURE 15.—UW 4006-306; pygidium, with pustulated axis, ×1.5.

FIGURE 16.—UW 4006-317; pygidium, ×1.

PLATE 4

Dikelocephalus minnesotensis Owen: from Arcadia, Trempealeau County, Wisconsin (A Aa). St. Lawrence Formation; heterolithic facies.

FIGURE 1.—UW 4006-305; pygidium, ×1.

FIGURE 2.—UW 4006-323; pygidium, counterpart, with unequally divided pleurae and relatively short posterolateral spine, ×0.75.

FIGURE 3.—UW 4006-310; pygidium, counterpart, with subequally divided pleurae, ×0.5.

Dikelocephalus minnesotensis Owen: from North Freedom Bed 2, Sauk County, Wisconsin (NF2). St. Lawrence Formation; heterolithic facies.

FIGURE 4.—UW 4006-102; cranidium, latex of counterpart, with long frontal area, pustulation, median tubercle, and relatively long palpebral lobes, ×1.

FIGURE 5.—UW 4006-205; cranidium, with short frontal area, ×1.

FIGURE 6.—UW 4006-119; cranidium, latex peel of counterpart, with median tubercle, ×0.75.
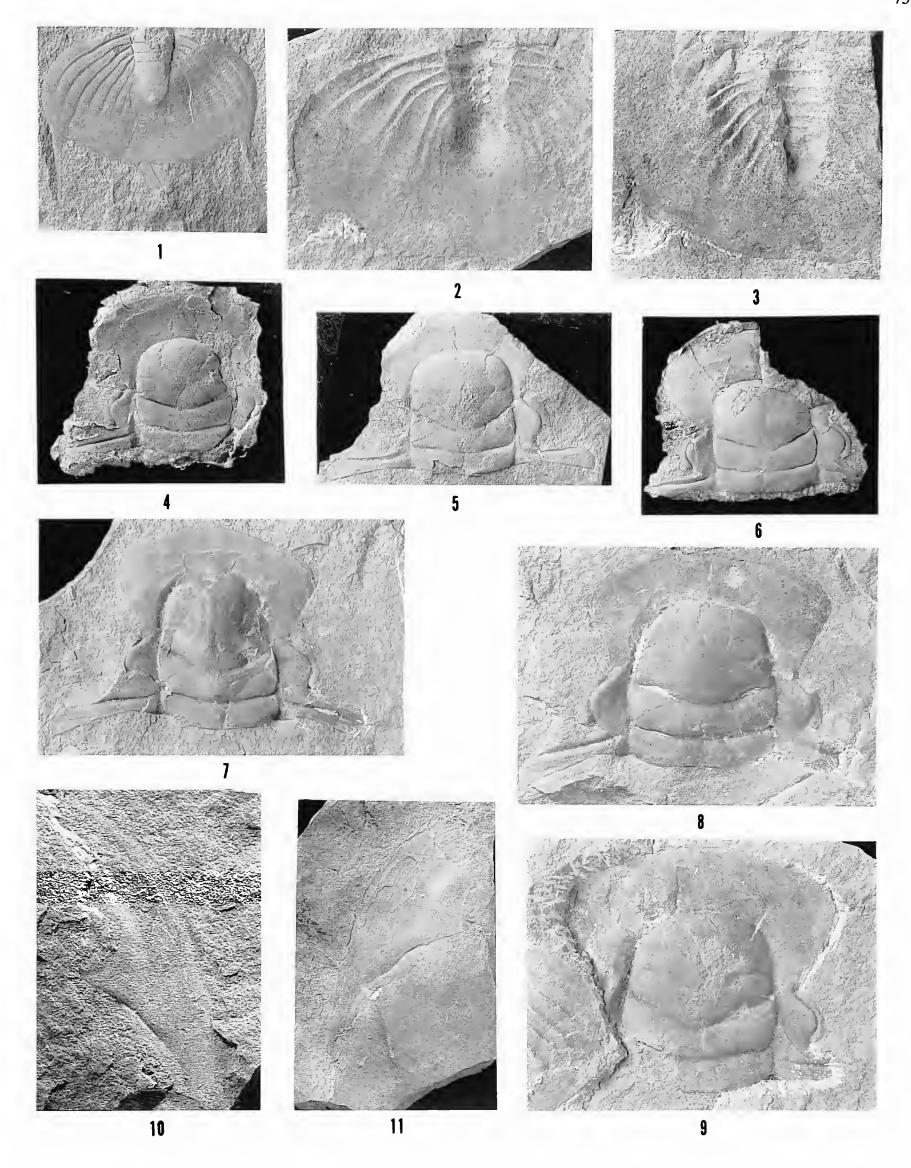
FIGURE 7.—UW 4006-236a; cranidium, with relatively small palpebral lobes, ×0.75.

FIGURE 8.—UW 4006-243; cranidium, ×0.75.

FIGURE 9.—UW 4006-190; cranidium, ×0.75.

FIGURE 10.—UW 4006-390; free cheek, ×1.5.

FIGURE 11.—UW 4006-388; free cheek, ×1.

PLATE 5

Dikelocephalus minnesotensis Owen: from North Freedom Bed 2, Sauk County, Wisconsin (NF2). St. Lawrence Formation; heterolithic facies.

FIGURE 1.—UW 4006-385; free cheek, with median suture, ×0.5.

FIGURE 2.—UW 4006-389; yoked free cheek with retracted cranidial anterior border, ×1.

FIGURE 3.—UW 4006-437; ventral view of hypostome, with maculae, ×2.

FIGURE 4.—UW 4006-402a; ventral view of hypostome, lacking maculae, ×1.

FIGURE 5.—UW 4006-"N8"; thoracic segment, from posterior of thorax, with ornament, ×2.

FIGURE 6.—UW 4006-196a; partial thorax and pygidium, with equally divided pleurae, ×1.

FIGURE 7.—UW 4006-411; pygidium, with long posterolateral spine, ×1.

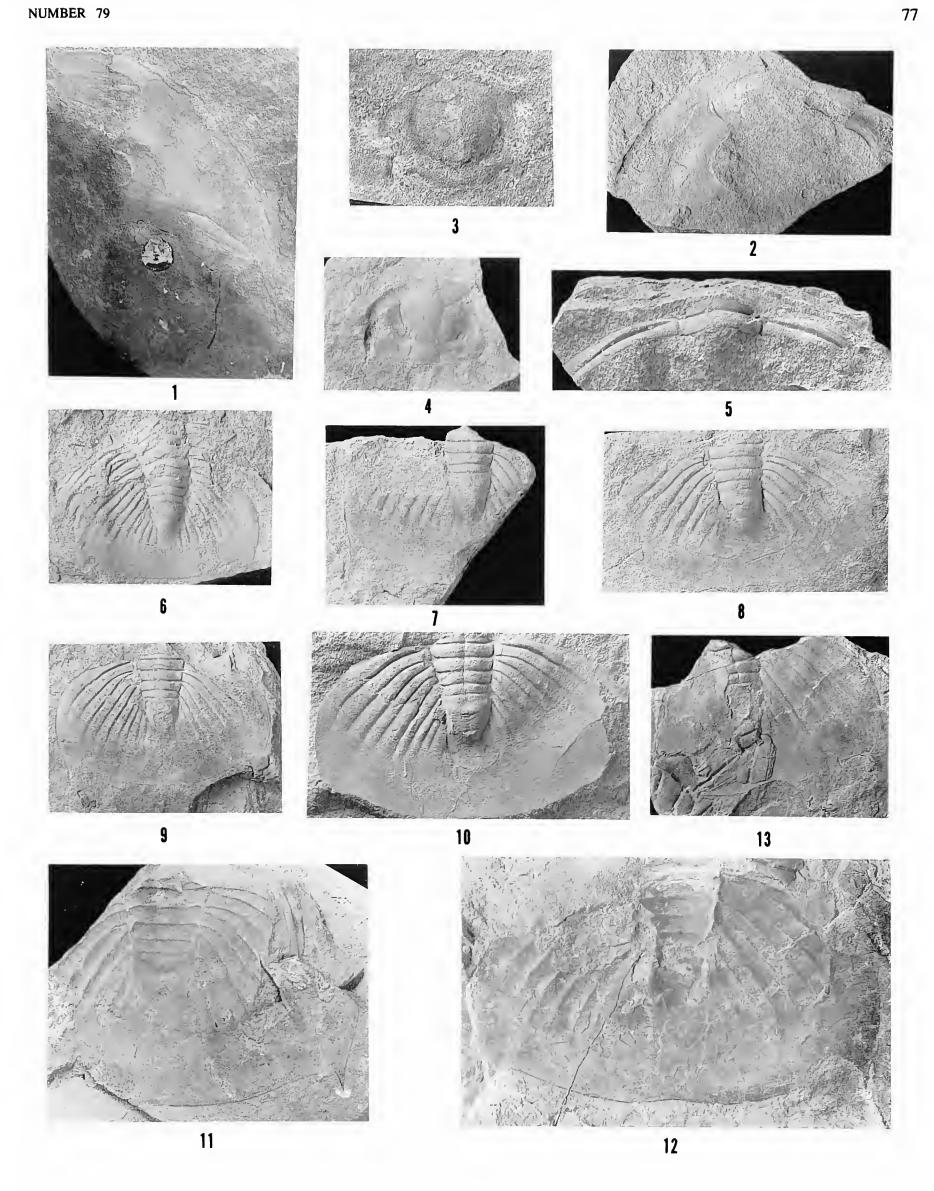FIGURE 8.—UW 4006-168; pygidium, with subequally divided pleurae, ×1.

FIGURE 9.—UW 4006-180a; pygidium, ×0.75.

FIGURE 10.—UW 4006-178b; pygidium, ×1.

FIGURE 11.—UW 4006-164; pygidium, counterpart with short posterolateral spine, ×1.

FIGURE 12.—UW 4006-170; pygidium, counterpart with short posterolateral spines and equally divided pleurae, ×0.75.

FIGURE 13.—UW 4006-142; pygidium, with unequally divided pleurae, ×0.5.

PLATE 6

Dikelocephalus minnesotensis Owen: from North Freedom Bed 8, Sauk County, Wisconsin (NF8). St. Lawrence Formation; heterolithic facies.

FIGURE 1.—UW 4006-1a; cranidium, with pustulation, ×3.

FIGURE 2.—UW 4006-130; cranidium, with pustulation and terracing on long frontal area, ×3.

FIGURE 3.—UW 4006-25a; cranidium, with pustulation, median tubercle, and deformed frontal area, ×2.

FIGURE 4.—UW 4006-17b; cranidium, latex peel of external mold, pustulated but lacking median tubercle, ×2.

FIGURE 5.—UW 4006-8; cranidium, latex peel of external mold, with pustulation and median tubercle, ×2.

FIGURE 6.—UW 4006-50a; cranidium, pustulated, ×2.

FIGURE 7.—UW 4006-19; cranidium, showing intercalated furrows and diminished pustulation, ×1.
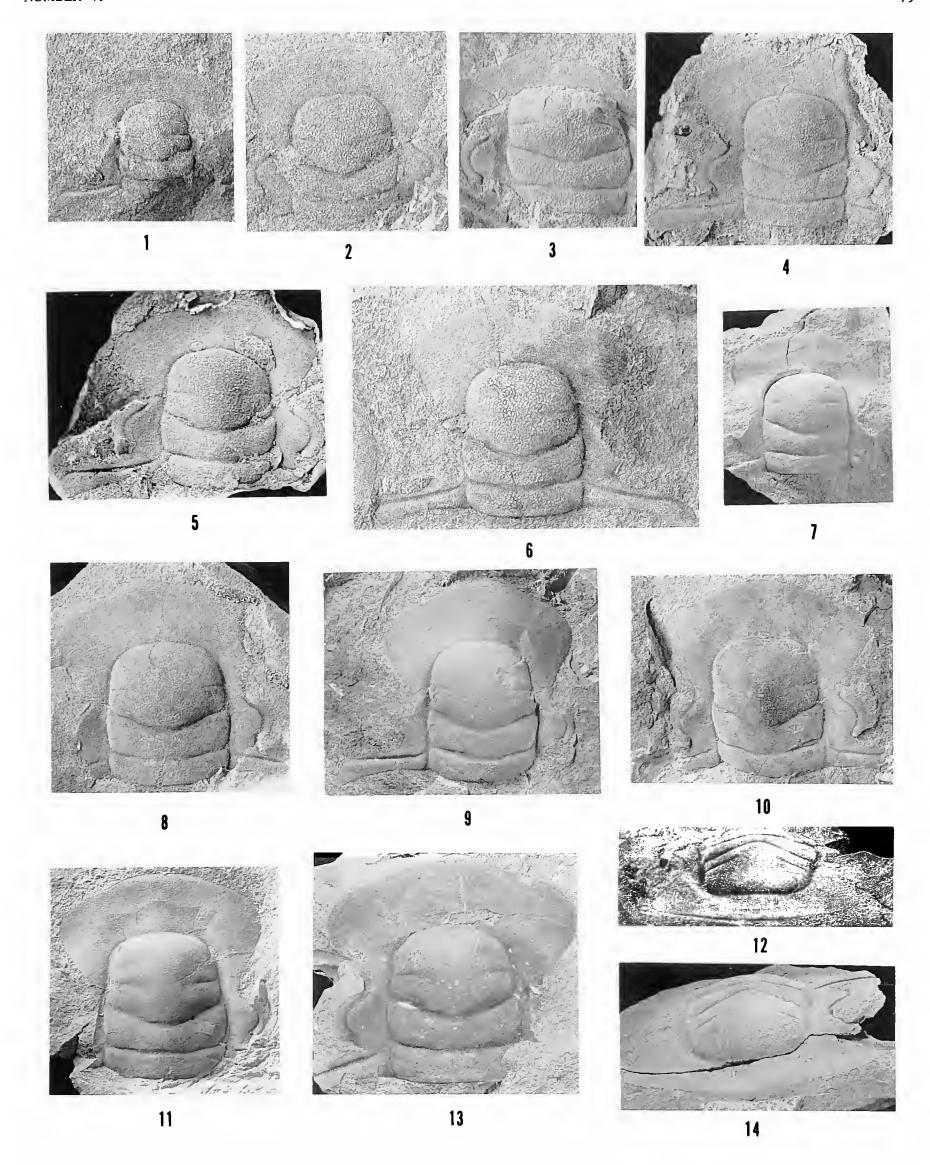
FIGURE 8.—UW 4006-32; cranidium, pustulated and with median tubercle. ×1.5.

FIGURE 9.—UW 4006-13; cranidium, with pustules diminished and restricted to axial region, ×1.

FIGURE 10.—UW 4006-77; cranidium, ×1.

FIGURES 11, 12.—UW 4006-52a; 11, cranidium, with median tubercle, pustulation absent, ×1; 12, anterior view of cranidium, ×1.

FIGURES 13, 14.—UW 4006-69; 13, cranidium, ×0.75; 14, anterior view of cranidium, ×0.75.

PLATE 7

Dikelocephalus minnesotensis Owen: from North Freedom Bed 8, Sauk County, Wisconsin (NF8). St. Lawrence Formation; heterolithic facies.

FIGURE 1.—UW 4006-69; lateral view of cranidium figured previously (Plate 6: Figures 13, 14), ×0.75.

FIGURE 2.—UW 4006-71; cranidium, very large with short palpebral lobe (anterior of which is damaged), ×0.5.

FIGURES 3, 4.—UW 4006-386; 3, free cheek, ×1; 4, lateral view of free cheek, ×1.

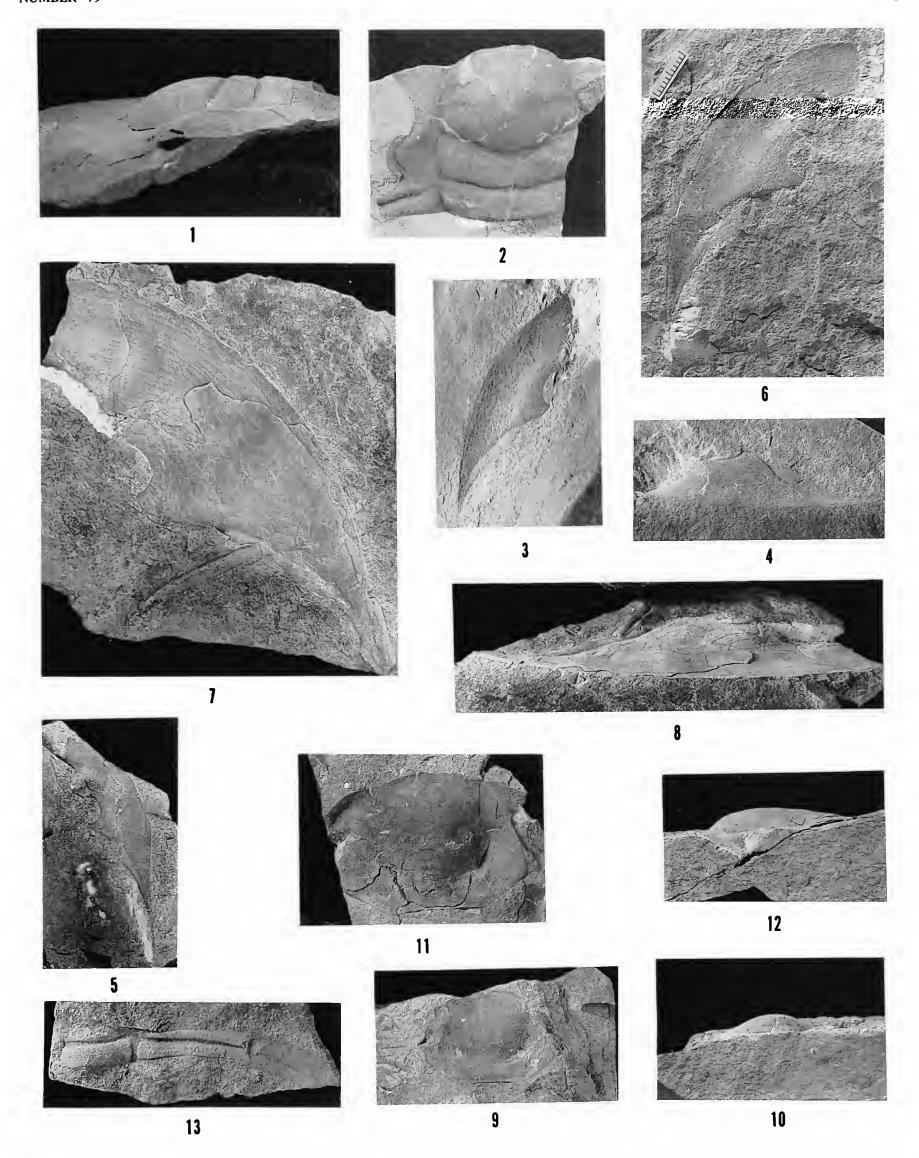FIGURE 5.—UW 4006-394; free cheek, with median suture, ×1.

FIGURE 6.—UW 4006-"N17"; free cheek, with median suture, ×1.

FIGURES 7, 8.—UW 4006-392; 7, free cheek, showing inosculate terraces on dorsal surface and broad doublure with straight terrace lines, ×0.75; 8, lateral view of free cheek, ×0.75.

FIGURES 9, 10.—UW 4006-430; ventral view of hypostome, ×1; 10, anterior view of hypostome, ×1.

FIGURES 11, 12.—UW 4006-422; ventral view of hypostome, ×1; 12, lateral view of hypostome, showing wing process extending dorsally, ×1.

FIGURE 13.—UW 4006-433; thoracic segment, ×1.

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PLATE 8

Dikelocephalus minnesotensis Owen: from North Freedom Bed 8, Sauk County, Wisconsin (NF8). St. Lawrence Formation; heterolithic facies.

FIGURE 1.—UW 4006-106; pygidium, showing pustulated axis, ×2.

FIGURES 2–4.—UW 4006-87: 2, pygidium, with long posterolateral spines and subequally divided pleurae, ×2; 3, posterior view of pygidium, ×2; 4, lateral view of pygidium, ×2.

FIGURE 5.—UW 4006-85; pygidium, with pustulated axis and long posterolateral spine, ×2.
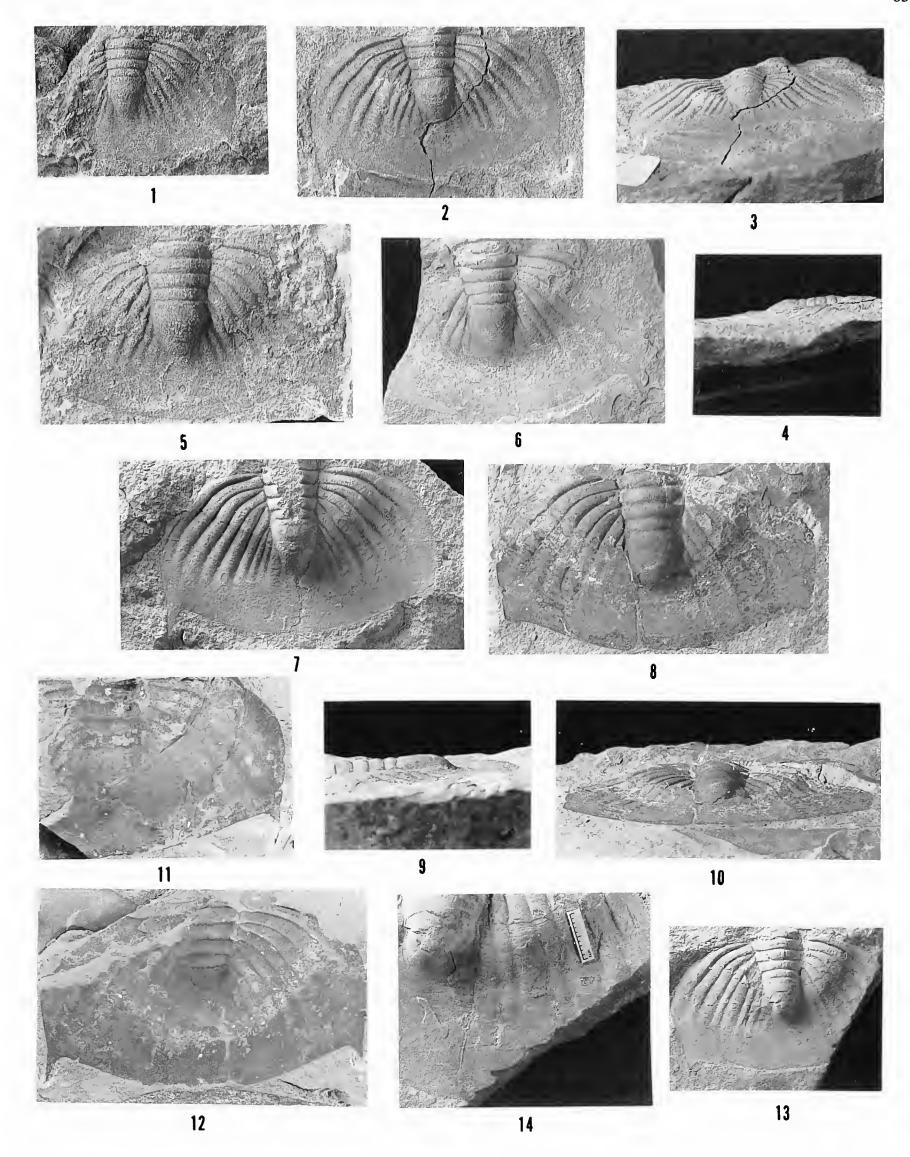
FIGURE 6.—UW 4006-91; pygidium, ×1.

FIGURE 7.—UW 4006-90a; pygidium, with equally divided pleurae and boring on doublure and dorsal surfaces, ×1.

FIGURES 8–10.—UW 4006-96; 8, pygidium, very large, with equally divided pleurae, ×0.5; 9, lateral view of pygidium, ×0.5; 10, posterior view of pygidium, ×0.5.
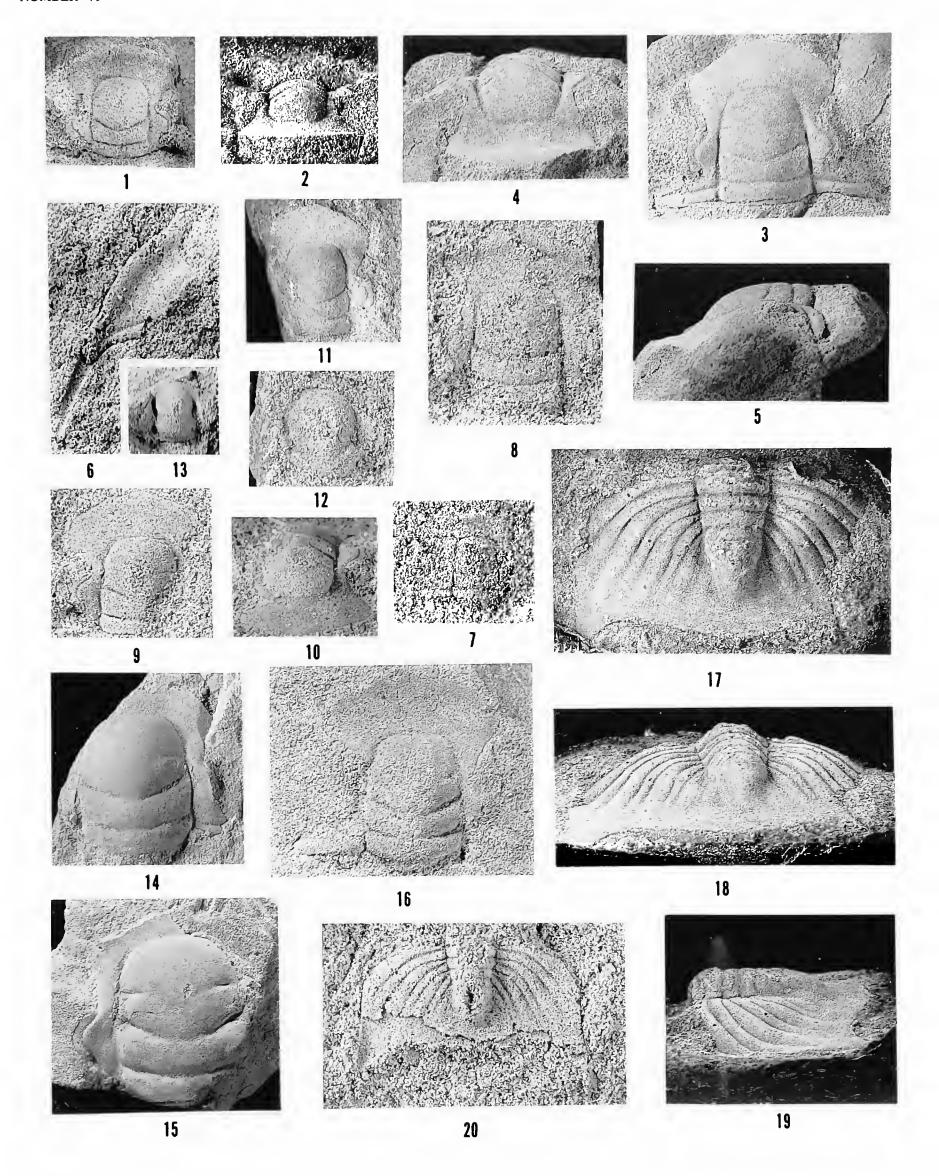
FIGURE 11.—UW 4006-97; counterpart of pygidium, with short posterolateral spine, ×0.75.

FIGURE 12.—UW 4006-505; counterpart of pygidium, ×0.75.

FIGURES 13, 14.—UW 4006-126; 13, pygidium, large with short posterolateral spine and unequally divided pleurae, ×0.5; 14, detail of the terrace lines on the ventral surface of pygidium, ×1.

PLATE 9

Dikelocephalus of unknown specific affinity. Reno Member, Tunnel City Group.

FIGURES 1, 2.—UMPC 6660a; 1, cranidium, ×1.5 (see Bell, Feniak, and Kurtz, 1952, pl. 38: fig. 4a); 2, antertior view of cranidium, ×1.5. Freeburg (FG), Houston County, Minnesota.

FIGURES 3–5.—UMPC 6660e, holotype of *Dikelocephalus freeburgensis*, Feniak; 3, cranidium, ×1 (see Bell, Feniak, and Kurtz, 1952, pl. 38: fig. 4e); 4, anterior view of cranidium, ×1; 5, lateral view of cranidium, ×1. Freeburg (FG), Houston County, Minnesota.

FIGURE 6.—UMPC 6660c; free cheek, ×3 (see Bell, Feniak, and Kurtz, 1952, pl. 38: fig. 4c). Hell Hollow (HW), Houston County, Minnesota.

FIGURE 7.—UMPC 9402e; cranidium, ×3. Hell Hollow (HW), Houston County, Minnesota.

FIGURE 8.—UMPC 9402c; cranidium, ×3. Hell Hollow (HW), Houston County, Minnesota.

FIGURES 9–10.—UMPC 9402b; 9, cranidium, ×2; 10, anterior view of cranidium, ×2. Hell Hollow (HW), Houston County, Minnesota.

FIGURE 11.—UW 4006-256; cranidium, ×1. Newton (NNa), Vernon County, Wisconsin.

FIGURE 12.—UW 4006-258; ventral view of hypostome, ×3, Newton (NNa), Vernon County, Wisconsin.

FIGURE 13.—USNM 473967; hypostome, ×2. Bean Hollow (BN), Vernon County, Wisconsin.

FIGURE 14.—UW 4006-272; cranidium, ×1. Lansing (LSb), Allamakee County, Iowa.

FIGURE 15.—UW 4006-273; cranidium, ×1. Lansing (LSb), Allamakee County, Iowa.

FIGURE 16.—UW 4006-270; cranidium, ×2. Exact locality unknown, perhaps Newton (NNa), Vernon County, Wisconsin.

FIGURES 17–19.—UMPC 6660f; 17, latex peel of external mold of pygidium, ×1.5 (see Bell, Feniak, and Kurtz, 1952, pl. 35: fig. 4); 18, posterior view of latex peel of pygidium, ×1.5; 19, lateral view of latex peel of pygidium, ×1.5. Freeburg (FG), Houston County, Minnesota.

FIGURE 20.—UMPC 6600b; pygidium, ×2 (see Bell, Feniak, and Kurtz, 1952, pl. 38: fig. 4b). Freeburg (FG), Houston County, Minnesota.

PLATE 10

Dikelocephalus of unknown specific affinity. Reno Member, Tunnel City Group.

FIGURE 1.—UW 4006-252; pygidium, ×1.5. Newton (NNa), Vernon County, Wisconsin.

FIGURE 2.—UW 4006-271; latex peel of pygidium, ×1.5. Newton (NNa), Vernon County, Wisconsin.

FIGURE 3.—UW 4006-256; latex peel of pygidium, ×1.5. Newton (NNa), Vernon County, Wisconsin.

FIGURE 4.—UW 4006-255; latex peel of pygidium, ×1.5. Newton (NNa), Vernon County, Wisconsin.

FIGURE 5.—UW 4006-257; latex peel of pygidium, ×1.5. Newton (NNa), Vernon County, Wisconsin.

FIGURE 6.—UW 4006-253; pygidium, ×1. Newton (NNa), Vernon County, Wisconsin.

FIGURE 7.—UW 4006-506; pygidium, ×3. Newton (NNa), Vernon County, Wisconsin.

FIGURE 8.—UMPC 9405a; pygidium, ×3. Hell Hollow (HW), Houston County, Minnesota.

FIGURES 9-11.—UW 4006-275; 9, pygidium, ×1; 10, posterior view of pygidium, ×1; 11, lateral view of pygidium, ×1. Lansing (LSb), Allamakee County, Iowa.
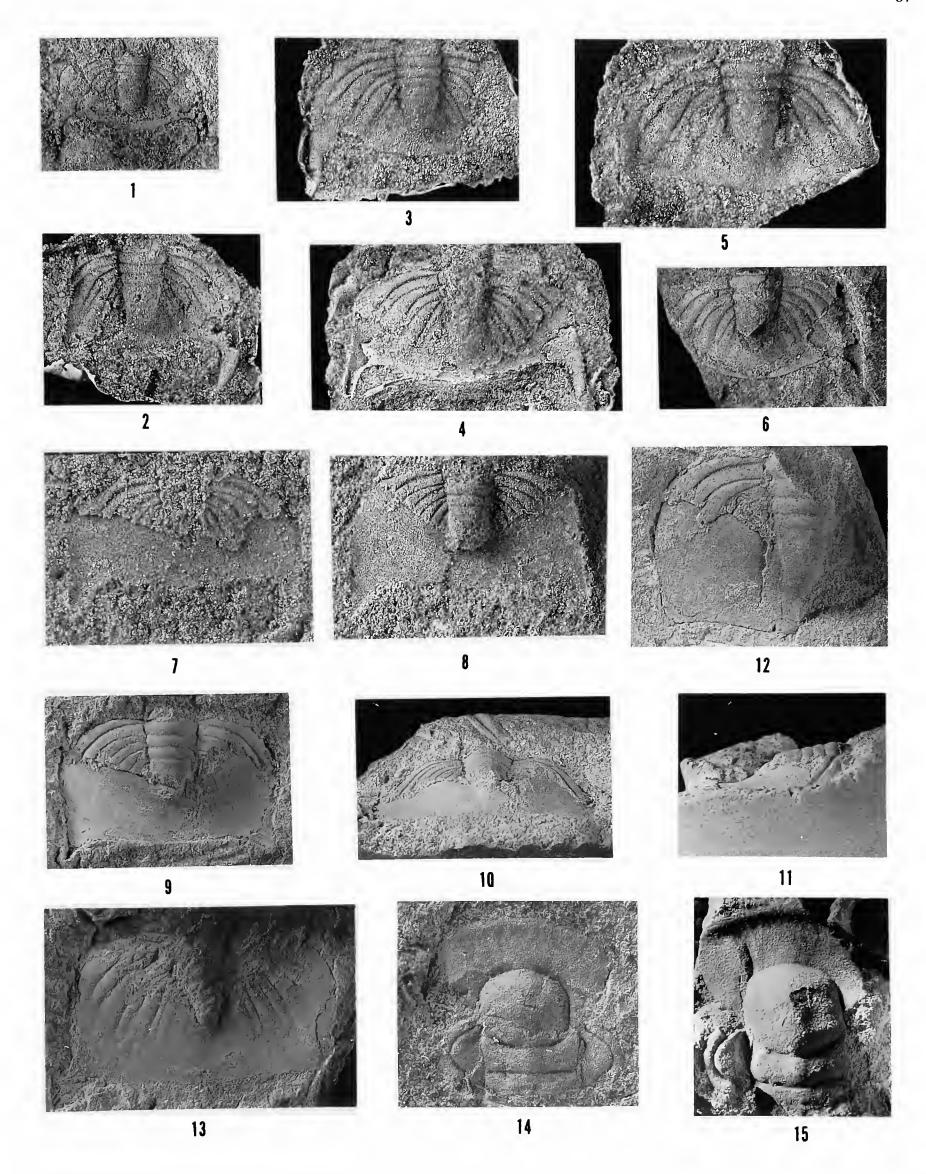
FIGURE 12.—UW 4006-274; pygidium, ×1. Lansing (LSb), Allamakee County, Iowa.

FIGURE 13.—UW 4006-463; pygidium, ×0.75. Excelsior (EX), Richland County, Wisconsin.

Dikelocephalus minnesotensis Owen: cranidia showing caeca from LaGrange Mountain (RWa), Goodhue County, Minnesota.

FIGURE 14.—AMNH 44020; cranidium, ×2.

FIGURE 15.—USNM 474688; cranidium, ×2.

PLATE 11

Dikelocephalus minnesotensis Owen: from various localities in the St. Lawrence Formation; heterolithic facies.

FIGURE 1.—USNM 474689; anterior of cranidium, ×1.5. 4 km north of Stoddard (near Victory), Vernon County, Wisconsin.

FIGURES 2–5.—UW 4004-1b; 2, cranidium, ×1; 3, two cranidia and counterpart of large pygidium, ×0.5; 4, marginal rim on pygidium, ×1; 5, post-axial emargination on pygidium, ×1. Galesville (GE), Trempealeau County, Wisconsin.

Dikelocephalus minnesotensis Owen: from St. Lawrence Formation; laminated sandstone subfacies.

FIGURE 6.—USNM 72711; cranidium, ×2. Myers Hill (MY), Monroe County, Wisconsin.

FIGURE 7.—USNM 58623; cranidium, ×1.5. Osceola (OA), Polk County, Wisconsin.

Dikelocephalus minnesotensis Owen: from St. Lawrence Formation; heterolithic facies.

FIGURES 8, 9.—AMNH 39094; 8, pygidium, ×0.5; 9, posterior view of pygidium, ×0.5. Madison (MS), Wisconsin.

Dikelocephalus minnesotensis Owen: from outside of the northern Mississippi Valley.

FIGURE 10.—USNM 447018; pygidium, ×1. Shale next to a normal fault of 1 m throw, 15 m east of curve sign on hillside at highway, about 100 m east of footbridge, 4.5 km east of footbridge at Glenwood, Glenwood Springs area, Colorado.

FIGURE 11.—USNM 447017; cranidium, ×1. Highland Peak Quadrangle, Pioche District, Nevada.

FIGURE 12.—GSC 75188; pygidium showing long posterolateral spines, ×2 (see Westrop, 1986, pl. 3: fig. 7). Mistaya Formation, southern Alberta Site 260.2.

FIGURE 13.—GSC 75208; pygidium, showing unequally divided pleurae, ×1. Mistaya Formation, southern Alberta Site 260.2.

FIGURE 14.—USNM 447016; cranidium showing pustulation, ×3. From "0.5 km above mouth of junction of ravine (entering) from east in river beds, Hudson Creek, Texas."
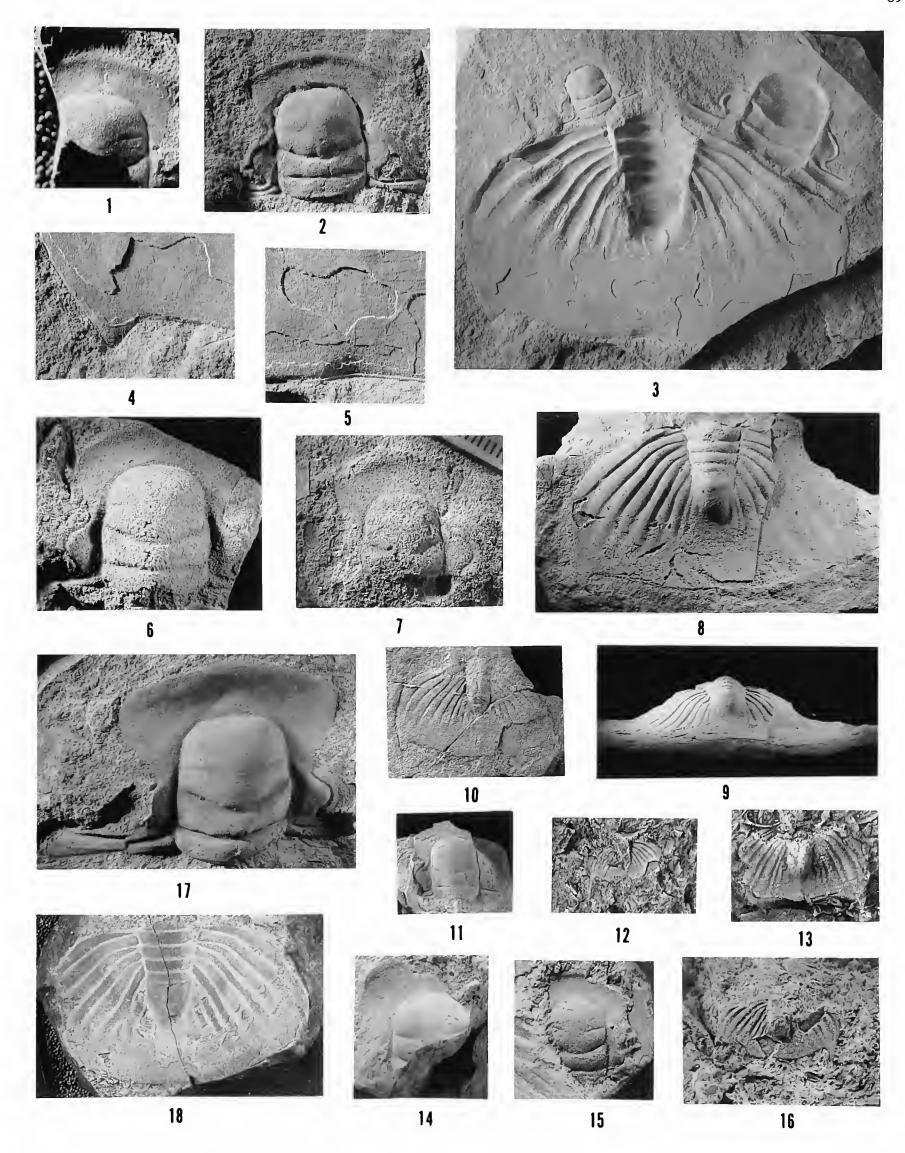
FIGURE 15.—USNM 447015; cranidium, ×3. From "0.5 km above mouth of junction of ravine (entering) from east in river beds, Hudson Creek, Texas."

FIGURE 16.—USNM 482957; pygidium, ×3. From northeast slope of Mount Lincoln, in limestone float above fault, Snake Range, Nevada.

Type specimens of *Dikelocephalus minnesotensis* Owen: from Stillwater (SWa), Washington County, Minnesota.

FIGURE 17.—USNM 447020; paralectotype cranidium, ×1 (see Owen, 1852, pl. 1: fig. 1).

FIGURE 18.—USNM 17863; lectotype pygidium, with abnormal division of the right posterior pleurae, ×0.5 (see Owen, 1852, pl. 1: fig. 1).

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